Departement für Kleintiere, Klinik für Zoo-, Heim- und Wildtiere
der Vetsuisse-Fakultät Universität Zürich

Direktor: Prof. Dr. med. vet. Jean-Michel Hatt

Arbeit unter Leitung von
PD Dr. med. vet. Marcus Clauss

Reproductive seasonality in captive wild ruminants: implications for biogeographical adaptation, photoperiodic control, and life history

Inaugural-Dissertation

zur Erlangung der Doktorwürde der
Vetsuisse-Fakultät Universität Zürich

vorgelegt von

Philipp Zerbe

Tierarzt
aus Offenbach a.M., Deutschland

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Inhaltsverzeichnis:

Zusammenfassung

Reproduktive Saisonalität in Menschenobhut gehaltener Wildwiederkäuer: Rückschlüsse auf biogeographische Adaptation, photoperiodische Kontrollmechanismen und weitere Anpassungen

Zur quantitativen Beschreibung der Reproduktionsmuster wurden Daten von 110 Wildwiederkäuerarten aus Zoos der gemässigten Zone verwendet (dabei wurde die Anzahl Tage, an denen 80% aller Geburten stattfanden, als Geburtenpeak-Breite [BPB] definiert). Diese Muster wurden mit verschiedenen biologischen Charakteristika verknüpft und mit denen von freilebenden Tieren verglichen.
Der Breitengrad des natürlichen Verbreitungsgebietes korreliert stark mit dem in Menschenobhut beobachteten BPB. Nur 11% der Spezies wechselten ihr reproduktives Muster zwischen Wildnis und Gefangenschaft, wobei für saisonale Spezies die errechnete Tageslichtlänge zum Zeitpunkt der Konzeption für freilebende und in Menschenobhut gehaltene Populationen gleich war.
Reproduktive Saisonalität erklärt zusätzliche Varianzen im Verhältnis von Körpergewicht und Tragzeit, wobei saisonalere Spezies für ihr Körpergewicht eine kürzere Tragzeit aufweisen. Rückschliessend ist festzuhalten, dass Photoperiodik, speziell die absolute Tageslichtlänge, genetisch fixierter Auslöser für die Fortpflanzung ist, und dass die Plastizität der Tragzeit unterstützend auf die erfolgreiche Verbreitung der Wiederkäuer in höheren Breitengraden wirkte.

Key words: Phänologie, Saisonalität, Reproduktion, Tragzeit, Photoperiodik

Abstract

Reproductive seasonality in captive wild ruminants: implications for biogeographical adaptation, photoperiodic control, and life history

A dataset on 110 wild ruminant species kept in captivity in temperate-zone zoos was used to describe their reproductive patterns quantitatively (determining the birth peak breadth [BPB] as the number of days in which 80% of all births occur); then this pattern was linked to various biological characteristics, and compared with free-ranging animals.
Globally, latitude of natural origin highly correlates with BPB observed in captivity, with species being more seasonal originating from higher latitudes. Kept in zoos, 89% of the species retained their reproductive pattern from the wild. For seasonal species, daylength at the time of conception between free-ranging and captive populations was similar.
Reproductive seasonality explains additional variance in the body mass–gestation period relationship, with more seasonal species having shorter gestation periods for their body size. We conclude that photoperiodism, and in particular absolute daylength, are genetically fixed triggers for reproduction that may be malleable to some extent by body condition, and that plasticity in gestation length is an important facilitator that may partly explain the success of ruminant radiation to high latitudes.

Key words: phenology, seasonality, reproduction, gestation, photoperiodism

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Reproductive seasonality in captive wild ruminants: implications for biogeographical adaptation, photoperiodic control, and life history

Philipp Zerbe[1,2], Marcus Clauss[1,*], Daryl Codron[1,3,4,5], Laurie Bingaman Lackey[6], Eberhard Rensch[1], Jürgen W. Streich[7], Jean-Michel Hatt[1] and Dennis W. H. Müller[1,8]

[1] *Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Winterthurerstrasse 260, 8057 Zurich, Switzerland*
[2] *Section for Small Animal Reproduction, Clinic for Animal Reproduction, University of Zurich, Winterthurerstrasse 260, 8057 Zurich, Switzerland*
[3] *Florisbad Quaternary Research, National Museum, Bloemfontein, 9300, South Africa*
[4] *School of Biological and Conservation Sciences, University of KwaZulu-Natal, Private Bag X01, Scottsville 3209, South Africa*
[5] *Department of Anthropology, University of Colorado at Boulder, Boulder, CO 80309, USA*
[6] *International Species Information System, 2600 Eagan Woods Drive, Suite 50, Eagan, MN 55121-1170, USA*
[7] *Leibniz-Institute for Zoo and Wildlife Research, Alfred-Kowalke-Strasse 17, 10315 Berlin, Germany*
[8] *National Park 'Bavarian Forest', Grafenau, Germany*

ABSTRACT

Many ruminant species show seasonal patterns of reproduction. Causes for this are widely debated, and include adaptations to seasonal availability of resources (with cues either from body condition in more tropical, or from photoperiodism in higher latitude habitats) and/or defence strategies against predators. Conclusions so far are limited to datasets with less than 30 species. Here, we use a dataset on 110 wild ruminant species kept in captivity in temperate-zone zoos to describe their reproductive patterns quantitatively [determining the birth peak breadth (BPB) as the number of days in which 80% of all births occur]; then we link this pattern to various biological characteristics [latitude of origin, mother-young-relationship (hider/follower), proportion of grass in the natural diet (grazer/browser), sexual size dimorphism/mating system], and compare it with reports for free-ranging animals. When comparing taxonomic subgroups, variance in BPB is highly correlated to the minimum, but not the maximum BPB, suggesting that a high BPB (i.e. an aseasonal reproductive pattern) is the plesiomorphic character in ruminants. Globally, latitude of natural origin is highly correlated to the BPB observed in captivity, supporting an overruling impact of photoperiodism on ruminant reproduction. Feeding type has no additional influence; the hider/follower dichotomy, associated with the anti-predator strategy of 'swamping', has additional influence in the subset of African species only. Sexual size dimorphism and mating system are marginally associated with the BPB, potentially indicating a facilitation of polygamy under seasonal conditions. The difference in the calculated Julian date of conception between captive populations and that reported for free-ranging ones corresponds to the one expected if absolute day length was the main trigger in highly seasonal species: calculated day length at the time of conception between free-ranging and captive populations followed a $y = x$ relationship. Only 11 species (all originating from lower latitudes) were considered to change their reproductive pattern distinctively between the wild and captivity, with 10 becoming less seasonal (but not aseasonal) in human care, indicating that seasonality observed in the wild was partly resource-associated. Only one species (*Antidorcas marsupialis*) became more seasonal in captivity, presumably because resource availability in the wild overrules the innate photoperiodic response. Reproductive seasonality explains additional variance in the body mass–gestation period relationship, with more seasonal species having shorter gestation periods for their body size. We conclude that photoperiodism, and in particular absolute day length, are genetically fixed triggers for reproduction that may be malleable to some extent by

* Address for correspondence (E-mail: mclauss@vetclinics.uzh.ch).

body condition, and that plasticity in gestation length is an important facilitator that may partly explain the success of ruminant radiation to high latitudes. Evidence for an anti-predator strategy involving seasonal reproduction is limited to African species. Reproductive seasonality following rainfall patterns may not be an adaptation to give birth in periods of high resource availability but an adaptation to allow conception only at times of good body condition.

Key words: phenology, seasonality, reproduction, gestation, photoperiodism, Bergmann's rule, Rensch's rule.

CONTENTS

I. INTRODUCTION

Habitats do not offer steady conditions to their inhabitants - they are exposed to climatic variations and environmental disasters. Some of these variations are unpredictable incidents such as cosmic or tectonic events, and life reacts to such phenomena rather than adapting to them. Other variations occur more or less regularly, but are nevertheless unpredictable - like the El Niño effect, or fruit mast years. To cope with such variations, species evolve mechanisms that allow for a plastic response of their behavioural patterns. A prerequisite of such behavioural plasticity is a fine detection mechanism that allows early sensing of the emerging event—especially if a response in reproductive output is adaptive. Examples for such adaptations are the reproductive patterns in kakapo (*Strigops habroptilus*) (Powlesland *et al.*, 1992) or dormice (*Glis glis*) (reviewed in Ruf *et al.*, 2006) that only reproduce during fruit mast years. By contrast, the whole life cycle of a species adapts (and does not just react) to regular and more or less predictable (periodical) environmental variations. One of the most important and best predictable variations is the seasonality in temperate zones, and its most reliable predictor is the variation in day length—photoperiodism—over the year (Bradshaw & Holzapfel, 2007). As an adaptation to seasonal changing of climate conditions within the temperate zone over the year, various animal species of all mammalian clades developed seasonal patterns of reproduction (Bronson, 1989). This allows for offspring to be born when food is available in abundance (which is important to ensure milk production), and the newborns to grow under favourable climatic conditions (Rutberg, 1984; Sinclair, Mduma & Arcese, 2000*b*; Santiago-Moreno *et al.*, 2006). Detailed studies have demonstrated that in several seasonal wild ruminants, earlier-born offspring can gain more weight and therefore survive the next winter better than later-born offspring (reviewed e.g. by

Côté & Festa-Bianchet (2001)). This seasonal reproduction is cued by photoperiodism (Bradshaw & Holzapfel, 2007), which, *via* the induction of melatonin release, modulates circadian and circannual pacemakers (Hazlerigg & Loudon, 2008; Dardene, 2012). Such physiological pacemakers are an active field of current research (e.g. Lincoln *et al.*, 2006; Hazlerigg & Lincoln, 2011; Hut & Beersma, 2011), but are not the topic of this review.

The seasonal reproduction of certain domestic species has important consequences for animal farming, as the reproduction rate of strictly seasonal species is more or less restricted to one reproductive cycle per year under the natural photoperiodic conditions of the northern hemisphere (Asher, Monfort & Wemmer, 1999; Rhind, Archer & Adam, 2002; Chemineau *et al.*, 2008). To overcome this limitation, artificial photoperiodic treatments are used to control reproduction in seasonal farm animals like sheep, goats and horses (Chemineau *et al.*, 2008). Reproductive seasonality must also be considered in conservation projects of endangered species. A thorough knowledge of the reproductive physiology (including seasonality) is a prerequisite for the successful use of assisted reproduction methods (gamete cryopreservation, artificial insemination, embryo transfer and *in vitro* fertilization) (Jabbour, Hayssen & Bruford, 1997; Sinclair, Ludwig & Clark, 2000*a*; Penfold, 2005; Santiago-Moreno *et al.*, 2006). The most famous example is the *ex situ* breeding program for the endangered giant panda (*Ailuropoda melanoleuca*), where monitoring of the female oestrus cycle during the short breeding season is used to decide when to introduce the male to the female, or when artificial insemination should be performed (Hodges *et al.*, 1984; Masui *et al.*, 1989).

To detect seasonal reproductive behaviour in the wild, the annual distribution of either mating or birthing events has to be observed. This might be difficult for many species that are either elusive or live in remote habitats, like duikers (Wilson, 2005) or chevrotains (Barrette, 1987; Nowak, 1991; Matsubayashi, Bosi & Kohshima, 2003). Birth records from zoological gardens offer very precise information about reproductive seasonality (Zuckerman, 1952; Brand, 1963; Pelt, 1967; Dittrich, 1970; Kirkwood, Gaskin & Markham, 1987; Skinner, Moss & Skinner, 2002), but it is not certain whether the reproductive seasonality of species in zoos reflects patterns of their conspecifics in the wild (Fairall, 1968). So far, only some exemplary comparisons of seasonality in reproduction between wild and captive populations have been published. It is described that some mammalian species with a fixed breeding season in temperate latitudes reverse their breeding season when transported to the Southern hemisphere, but demonstrate the same breeding season or an irregular pattern when transported to the tropics (e.g. Marshall, 1937; The Duke of Bedford & Marshall, 1942; Zuckerman, 1952; Brand, 1963; Caughley, 1971; Spinage, 1973; Fletcher, 1974; Paré, Barrette & Prescott, 1996; Skinner *et al.*, 2002). As most zoos are located within the temperate zone of the Northern hemisphere with its distinct seasons, but provide food in sufficient amounts and quality throughout the year, an analysis of reproductive seasonality of wild species in captivity may provide further insights into the regulating mechanisms of reproductive seasonality. For example, Skinner *et al.* (2002) suggested that the change of the sable antelope (*Hippotragus niger*) from a seasonal breeder in the wild to a non-seasonal breeder in captivity could be explained by the continuous feeding regime in the zoo. Pelt (1967) had already presented a similar observation and interpretation due to a comparison of free-ranging and captive blackbuck (*Antilope cervicapra*), and Piening Schuler *et al.* (2009) made similar observations for several gazelle species. On the other hand, the finding that some gazelles that were considered aseasonal breeders, with a seasonal birthing pattern in the wild putatively due to seasonal fluctuations in forage availability, retained their seasonal reproduction in captivity under constant diet provision (Flower, 1932), led to the conclusion that there actually was an underlying photoperiodic response that determined the observed birthing patterns.

The above studies, as well as observations from the wild, mainly provide categories to describe the seasonality of reproductive behaviour (e.g. seasonal *versus* non-seasonal), or describe the monthly distribution of birth events (e.g. Spinage, 1973; Skinner *et al.*, 2002). Even though quantitative, the monthly distribution of births often does not allow for a comparison between different species, because the degree of seasonality is not sufficiently resolved. A species that may give birth to half of the annual offspring in the last week of March and the other half in the first week of April demonstrates the same monthly distribution of births (i.e. 50% in March and in April) as a species that delivers all the annual offspring in March and April but with an even distribution of birthing during the whole months. The first species is, however, notably 'more' seasonal than the second one. Such analyses of the degree of seasonality across different species are needed to test for factors that influence reproductive seasonality. Unfortunately, the generation of such comparative data requires a very close monitoring of whole populations (i.e. a precise documentation of all births within a population), and sufficient data from the wild are therefore mostly not available.

The situation for data of captive-born animals is completely different. The International Species Information System (ISIS) is an institute of the international zoo community that has collected stock data of participating zoos (approximately 750 worldwide) over the last 35 years. These data include the exact dates of birth of almost all individuals born in captivity since 1980. This collection therefore provides data on birth dates in a previously unknown quantity, facilitating a quantitative analysis of reproductive seasonality.

Here, we introduce an expression of reproductive seasonality as a continuous variable, to increase the power of comparative analyses. The following hypotheses then guided our approach.

(1) The degree of seasonality in wild ruminants depends on a variety of factors:

(a) Birth seasons become shorter, i.e. animal species become more seasonal, with increasing latitude of their geographical origin, due to a shortening of the season of favourable conditions to raise offspring with increasing latitude (Rutberg, 1987).

(b) The mother-young relationship (hider *versus* follower; Lent, 1974) influences the degree of birth seasonality. It was described that 'follower' species (offspring immediately follows mother after birth, and often joins the herd) have consistently shorter birth seasons when compared with 'hider' species (offspring is hidden during the first days of life) (Rutberg, 1987; Sinclair *et al.*, 2000*b*). This pattern was interpreted as an adaptation to prevent predation. Estes (1976) showed that wildebeest (*Connochaetes taurinus*) calves suffered a lower mortality when born at the peak of the calving season and suggested therefore that birth synchrony was an anti-predator strategy. Similar findings were reported for caribou (*Rangifer tarandus*) (Dauphiné & McClure, 1974; Adams, Singer & Dale, 1995), moose (*Alces alces*) (Testa, Becker & Lee, 2000), wapiti (*Cervus elaphus*) (Smith & Anderson, 1998), roe deer (*Capreolus capreolus*) (Panzacchi *et al.*, 2008) and pronghorn (*Antilocapra americana*) (Gregg *et al.*, 2001). First, the sheer number of young may prevent predators from taking a significant fraction of all newborns when compared to species with non-seasonal reproduction (instantaneous saturation). Second, many adults breeding synchronously may protect their offspring better using group defence in follower species. Third, the presence of many young in a herd may interfere with a predator's ability to pick and pursue a specific target (confusion). Such adaptations are less relevant for hiding species, whose offspring are less vulnerable to predation when compared to offspring that immediately follows their mothers through more open habitats (Rutberg, 1987). Hiders, by contrast, rely on low encounter rates between predators and neonates. In such species, a short birthing season could even be considered disadvantageous, because it would increase the likelihood that roaming predators encounter neonates at a certain period of time, thus promoting adaptations to increase searching activities in this particular time period (Rutberg, 1987). Hiders should therefore benefit from an asynchronous birthing pattern (Ims, 1990*a*, *b*). Because such an asynchronous birthing pattern is unlikely to occur at high latitudes, the hider-follower distinction should be particularly relevant for less-temperate species, such as the African ruminant community.

(c) The feeding strategy (browser *versus* grazer) influences the degree of birth seasonality. African grazers should have shorter birth seasons compared to browsers, as grasses in rain-dependent regions tend to experience a shorter flush than the deeper-rooted browse plants. This shorter time span in which high-quality food is available for grazers should select for greater birth synchrony (Leuthold & Leuthold, 1975; Skinner *et al.*, 2002). This theory was rejected by Rutberg (1987) for the categorical variables browser *versus* grazer and seasonal *versus* non-seasonal species for a global dataset; Kiltie (1988) also found no support for this hypothesis in another global dataset. A decisive factor in this respect could be that differences between browsers and grazers might be more pronounced in the African biome, due to specific adaptations to the presence of C4 grasses (Codron *et al.*, 2008*a*; Codron & Clauss, 2010).

(d) The mating system (monogamous *versus* polygamous) is associated with the degree of birth seasonality. Polygamous species should be more seasonal than monogamous species. Monogamous males that live in close proximity to their (single) partner throughout the year do not have to cope with the problem of finding the female when it is in oestrus. By contrast, males of polygamous species attempt to copulate with as many females as possible, resulting in higher sexual competition amongst the males. Thus, it might be advantageous if all females are in oestrus at the same time, limiting the time period of high reproductive investment for the males (Lane *et al.*, 2010); in other words, reproductive seasonality might facilitate polygamous mating systems. Because the degree of sexual dimorphism correlates positively with mating system in ruminants (Alexander *et al.*, 1979; Jarman, 1983; Weckerly, 1998; Loison *et al.*, 1999), we therefore also expect more seasonal species to have a higher degree of male-biased sexual dimorphism.

(2) Differences between the wild and captivity can help to explain parts of the mechanisms that lead to seasonal reproductive patterns:

(a) Species that originate from a different hemisphere than the one they are kept in switch their seasonal birth pattern accordingly (Marshall, 1937; Zuckerman, 1952; Brand, 1963; Caughley, 1971; Spinage, 1973; Fletcher, 1974; Lincoln, 1985; Paré *et al.*, 1996; Skinner *et al.*, 2002).

(b) Species with a distinct seasonal reproductive pattern, that originate from a different latitude than the one they are kept in, should conceive

when the absolute daylength at the location where they are kept is similar to the absolute day length of breeding in their natural habitat. Because day length changes across the year with latitude, this implies a shift in breeding events in relation to the calendar year (Fig. 1). The direction of this shift depends on two factors—whether the species is kept at lower or higher latitudes than their natural origin, and whether breeding is usually triggered before or after equinox (Fig. 1). Rutberg (1987) predicted such a shift in the timing of reproductive activity between populations at different latitudes. If day length is the triggering photosignal for the initiation of mating or conception, then differences in conception patterns between the wild and captivity should be of such a magnitude that the absolute day length in the wild (x) and in captivity (y) at the initiation of reproductive activity is identical ($y = x$). Evidence for or against such a mechanism so far stems mainly from intraspecific comparisons and is somewhat ambiguous. On the one hand, several authors suggest that within a species, latitude does not influence this pattern (Fletcher, 1974; Paré *et al.*, 1996; Moe, Rutina & Du Toit, 2007); on the other hand, many other authors demonstrate that such a pattern exists (Ransom, 1966; Fairall, 1968; Sadleir, 1969; Nievergelt, 1974; Bunnell, 1982; fig. 5 in Bronson, 1985; Rutberg, 1987 cites several comparisons of populations in East Africa and South Africa; Saether *et al.*, 1996; Flood & Tedesco, 1997; Linnell & Andersen, 1998; Bonenfant *et al.*, 2004; Loe *et al.*, 2005; several examples in Santiago-Moreno *et al.*, 2006; Ungerfeld *et al.*, 2008). In the case of the red deer (*Cervus elaphus*), the direct conflict of reports (Fletcher, 1974; Bonenfant *et al.*, 2004; Loe *et al.*, 2005) makes this question particularly interesting. In the case of the Himalayan tahr (*Hemitragus jemlahicus*), a change of the birthing pattern with latitude would be obvious if one single outlier (out of seven populations) was excluded from the published analysis (*cf.* fig. 2 in Paré *et al.*, 1996). Alternatively, if absolute day length was not important in ruminants, and breeding was mainly triggered by changes in day length only (as commonly assumed for long-lived animals; Bradshaw & Holzapfel, 2007), then no systematic offset of reproductive events between free-ranging and captive populations should be discernible.

(c) Species expand their breeding season or change from a seasonal to a non-seasonal breeding pattern due to the reduced selective pressure (no predation) or the unlimited water and/or food supply in captivity (Caughley, 1971; Skinner *et al.*, 2002; Piening Schuler *et al.*, 2009). Intraspecific comparisons of birthing patterns between habitats of different quality, between animals of different body condition, or differences in resource availability between years suggest that a higher resource availability, *via* a quicker attainment of a high nutritional status, facilitates earlier mating and birthing seasons, even if the general onset of reproductive activity is still determined by photoperiod (Verme, 1965, 1969; Nievergelt, 1966; Mitchell & Lincoln, 1973; McGinnes & Downing, 1977; Hamilton & Blaxter, 1980; Flydal & Reimers, 2002; Post, 2003). Correlations of rainfall patterns and food quality with mating/birthing events in less pronounced seasonal species support this concept (Moe *et al.*, 2007). Correspondingly, we additionally expect that those species that maintain a seasonal reproductive pattern in captivity enter into reproductive activity somewhat earlier than in the wild due to their putatively better nutritional status; in other words, for the model suggested above with day length in the wild (x) and in captivity (y) at the initiation of reproductive activity, we predict a relationship of $y = 1.0\ x + a$ due to a systematic forward shift of reproduction due to unlimited food supply. In other species, which show a moderate seasonality in the wild, we expect the high levels of nutrition in captivity to result in disappearance of a seasonal reproduction pattern (Montgomery, Scott & Hudson, 1985).

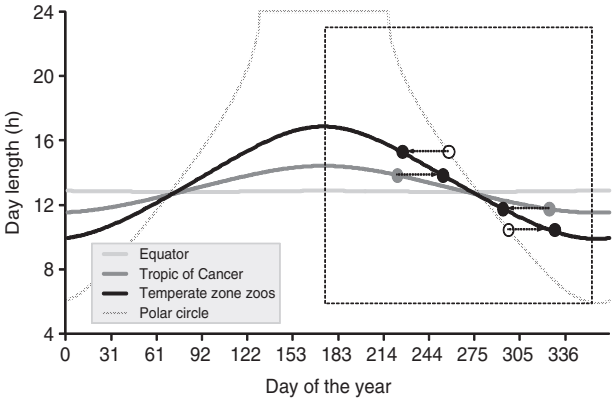

Fig. 1. Day length (including civil twilight) of each day of the year at different latitudes (calculated according to Forsythe *et al.*, 1995). The window of the mating season (boxed area) is indicated for short-day breeders (i.e. animals that mate during the period of the year when day length decreases). If mating was triggered by a day length threshold, we would expect species originating from higher latitudes than the one they are kept at to start reproducing sooner in captivity than in the wild if the day length threshold is before equinox, but later than in captivity if the day length threshold is after equinox. For species originating from a lower latitude than the one they are kept at, the opposite pattern should apply.

(3) Reproductive seasonality is associated with other life-history parameters that help facilitate the respective patterns: seasonal species adjust their gestation period length so that offspring are born at times that ensure maximum offspring survival; therefore, seasonality can partly explain the residual variation in the relationship between body mass and length of the gestation period (Müller *et al.*, 2011*b*). The gestation period of artiodactyls scales to body mass$^{0.16\pm0.03SD}$ (Western, 1979). The variation in this relationship might derive in part from the fact that larger animals shorten, and smaller animals lengthen their gestation period in relation to body mass in order to achieve birthing at a beneficial time of the year at high latitudes. This concept was elaborated in detail by Kiltie (1984, 1988) who also suggested that species in which gestation times exceed the time between two seasonal periods of high resource availability might be excluded from reproducing (and hence living) competitively at higher latitudes. As this author notes, the (historical) occurrence of species with gestation periods longer than 1 year—perissodactyls, proboscids and camelids—at higher latitudes indicates that a reproductive biology characterised by short gestation periods is not a *conditio sine qua non*, but should be considered one of many possible adaptations to life at high latitudes.

II. METHODS

We used data of approximately 200000 animals representing 110 different species of captive ruminants (suborder Ruminantia) from the International Species Information System (ISIS) data files. The observation interval was between 1980 and 2006. We removed species that had their last recorded birth before 1997 (e.g. that were no longer kept in ISIS zoos), or had an overall birth-count below 90. Only records with an exact birth date and from countries of the northern hemisphere with distinct seasons (spring, summer, autumn and winter) were used, i.e. we generally excluded animals from zoological collections of the Arabian Peninsula, Australia, Asia (except for Japan), Mexico, South America and Africa. Exceptions to this rule are explicitly mentioned. Years were sub-divided into 73 consecutive 5-day intervals, and the total number of births that occurred within each interval was counted. For leap years, births from December 31st were allocated to the 73rd interval. As there was a salient increase of births on January 1st, which was most likely the effect of the reporting management of some zoos, the first interval of the year was calculated as the average of the second and preceding 73rd interval. This effect was noticeable in 33 of the 110 species. We are aware of the fact that some zoos proactively time breeding of their animals to prevent births in certain seasons of the year; however, to our knowledge, this strategy is not applied universally, neither on a species nor on a zoo level. On the other hand, zoos may actively prevent breeding by separation or medical contraception. Although this is rare in wild ruminants, such procedures will impact the reproductive output; however, this should not affect results on reproductive seasonality.

For the comparison of seasonality patterns between the wild and zoo data, we had to introduce a categorical variable in order to accommodate literature data for free-ranging populations. Species were allocated subjectively, based on their birthing patterns, to five categories (Fig. 2): Category 1: narrow peak (less than approximately 60 days), no births for the rest of the year. Category 2: expanded peak (<60 days) or double peak, no births for the rest of the year. Category 3: peak(s) with small number of births throughout the year. Category 4: births throughout the year, undulating pattern (possibly indicating preferred seasons). Category 5: constant births throughout the year without a clear preferred season.

In order to allocate species from captivity to category 4 or 5, at least 150 birth events were required. Due to the concentration of birth events within a rather short time period in more seasonal species (categories 1–3), 90 birth events were considered sufficient for an allocation into these categories (*cf.* a similar observation on the number of birth records required for seasonal and aseasonal species by Zuckerman, 1952).

Data on categorical birth seasonality in the wild, mid-latitude of geographical origin, body mass, sexual size dimorphism, mating type, mother-young relationship, proportion of grass in the natural diet, and the length of the gestation period, were taken from the literature (online Appendix S1). We used data on the start of the birthing period in combination with the gestation length of the respective species to calculate the start of the mating/conception season in captivity, and in the wild. Because transitions between the seasonality categories are to a degree subjective, a change of more than 1 category was considered as a true change in the seasonality pattern when comparing seasonality categories between free-ranging and captive populations. The day length of a specific day of the year, at a specific latitude, was calculated, including civil twilight (which is defined as the time between sunrise or sunset and when the centre of the sun is six degrees below the horizon; light during civil twilight is bright enough to perform ordinary outdoor activities without artificial light), according to Forsythe *et al.* (1995). For these calculations, the mean latitude of captive populations was assumed to be 45°. For the overall relationship with reproductive seasonality, we used the median latitude of origin for species given in the PanTHERIA database (Jones *et al.*, 2009; online Appendix S1); we appreciate that using the median of the range given in this database introduces a source of error in the dataset, because the core area of origin for many species will not be in the middle of their reported range; it should be noted, however, that this source of error is not *a priori* systematic. For the comparison of the day length at which mating/conception occurred in the wild and in captivity (which included only species with a BPB80 < 33 days; see Section III.5), we used data on individual free-ranging populations from the literature for which the exact latitude was noted (online Appendix S2). The date of mating/conception was calculated using literature

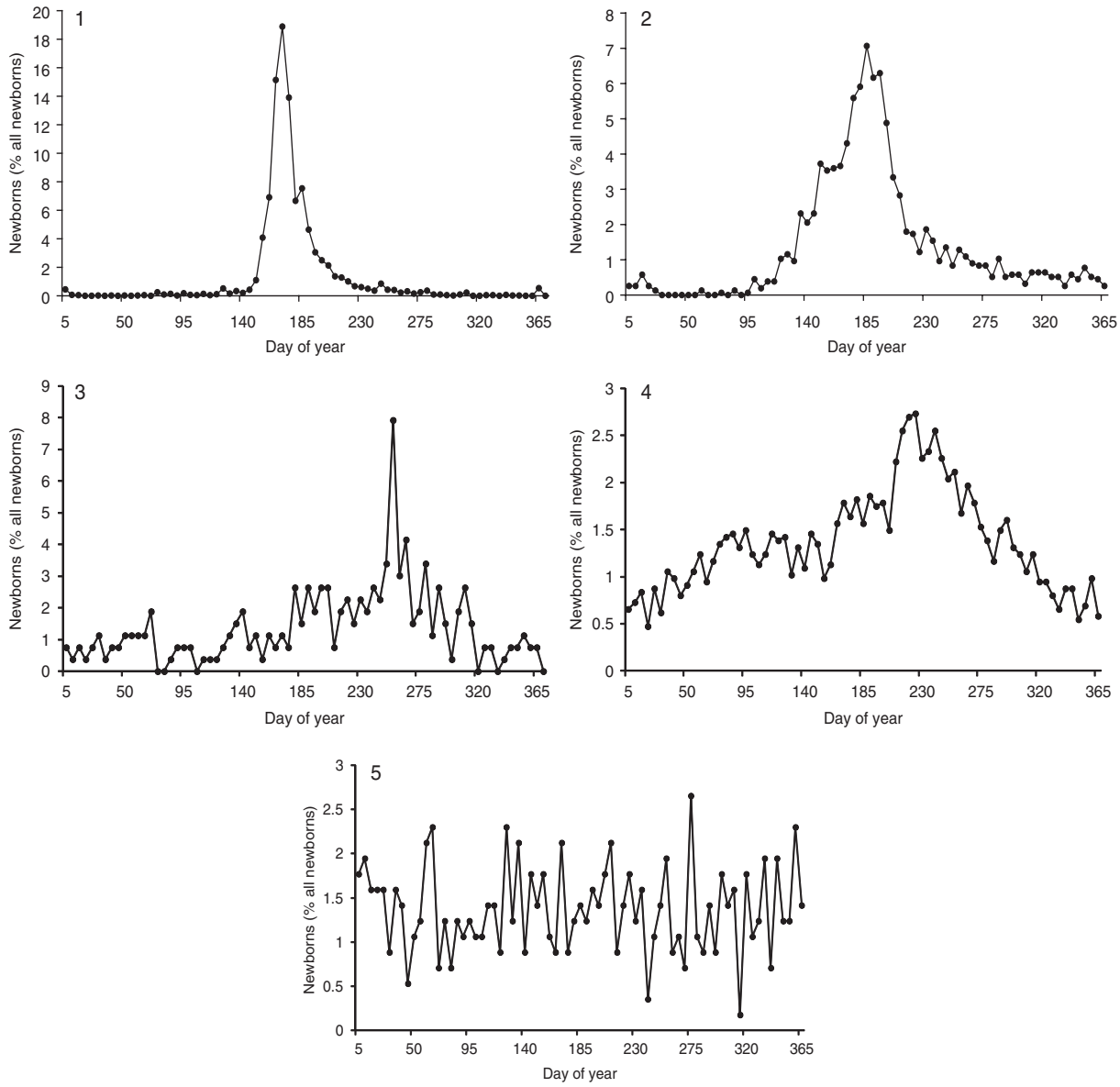

Fig. 2. Classification of seasonality categories according to the pattern of birth distributions across the year (as divided into 5-day blocks) from 1: highly seasonal to 5: aseasonal species. 1, *Dama dama*; 2, *Connochaetes taurinus*; 3, *Nanger soemmeringii*; 4, *Nanger dama*; 5, *Tragulus javanicus*.

reports on the birthing pattern of the species and re-calculating conception by subtracting the gestation period. The literature sources for Appendices S1-3 are collated in Appendix S4.

As a quantitative measure of the degree of reproductive seasonality, we defined the birth peak breadth (BPB) as the number of days (calculated as 5-day intervals) in which a certain percentage (50, 70, 80 and 90%; BPB50, BBP70, BPB80 and BPB90, respectively) of all births occurred (adapted from Rutberg, 1987). A command line script ('peakfinder', cross platform Perl script) was developed to search for the smallest number of successive intervals that included the demanded percentage of births (Fig. 3). When there was more than one such birth peak (i.e. same number of 5-day intervals), we used the window with the highest number of births for further analyses.

Comparisons between ruminant subfamilies were performed using a one-way analysis of variance (ANOVA) with *post hoc* tests using Sidak adjustment for multiple comparisons. Nonparametric correlations were analyzed by Spearman's ρ and parametric correlations by Pearson's R. To analyze the influence of external and physiological factors on seasonality, body mass, latitude of geographical origin, mating type or sexual dimorphism, mother-young relationship, proportion of grass in the natural diet, and whether or not a species was of African origin, we included and then excluded these factors or covariates in a backward stepwise general linear model approach, including two-way interactions. Because the interaction of African species and latitude, and the interaction of African species and the mother-young relationship were significant in the resulting model (data not shown), and because several predictions

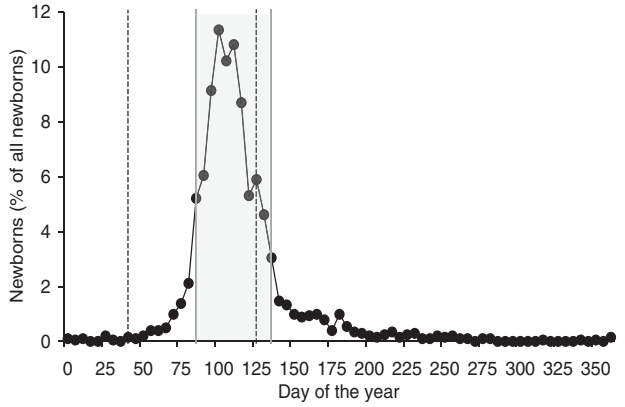

Fig. 3. Different approaches to determine the degree of reproductive seasonality in Père David's deer (*Elaphurus davidianus*). The dotted lines indicate start and end of the 80% birth approach by Rutberg (1987), defined as the time period in which 80% of all births take place from the beginning of the first birthing activity onwards, and the solid gray lines delineate the shaded grey area that denotes the birth peak breadth (BPB80), defined as the shortest time period in which 80% of all births take place. Note the better representation of the real reproductive pattern by the BPB approach.

referred to African or non-African species specifically, we decided to perform the following analyses on three datasets—the total dataset, African species, and non-African species. We report results of various linear models in which specific cofactors were tested; we also report the final linear model for every dataset in which non-significant factors were successively excluded (without interactions). To achieve normality, body mass was log-transformed in advance. To test the hypothesis that animals evolved changes in their gestation period length to adapt to a seasonal environment, another backward stepwise linear model was used in which the length of the gestation period was the dependent variable, and body mass, seasonality (as BPB80), mating type or sexual dimorphism, mother-young relationship, and proportion of grass in the natural diet were included as independent variables or cofactors, respectively. We used the relative gestation length (in days body mass$^{-0.12}$; exponent derived from linear regression analysis from log-transformed gestation length and body mass) for a graphical representation of the results.

In order to avoid false interpretation of ancestry-based correlations in these models as adaptations (i.e. finding a significant result simply because related species behave in a similar manner) (Felsenstein, 1985; Pagel, 1999), the analyses were not only performed as ordinary least squares (OLS), but also controlled for phylogenetic influences using the phylogenetic generalized least-squares method (PGLS) (Martins & Hansen, 1997; Rohlf, 2001). The phylogenetic tree was derived by pruning the mammal supertree from Bininda-Emonds *et al.* (2007) for those species not represented in the dataset, using Mesquite (Maddison & Maddison, 2006). Missing taxa were included ['*Gazella arabica*' was managed as one population by the zoo community but is in fact a hybrid population; *Ovis orientalis* was split into three subspecies (*O.o.musimon, O.o.gmelini, O.o.vignei*) as the start of their breeding seasons differ markedly from each other] and polytomies were resolved (see online Appendix S3 for the phylogenetic tree used). Because the resulting tree was not based on our own calculations of branch lengths using consistently the same characters, we used only a tree without branch lengths. The statistical calculations were performed with PASW 18.0 (SPSS Inc., Chicago, IL, USA) and COMPARE 4.6 program (Martins, 2004). The significance level was set to $P < 0.05$. Differences in significance between OLS and PGLS are indicated in results tables by grey shading.

III. RESULTS

(1) Relationships in the basic ruminant dataset

In our dataset, there was no significant relationship between (log-transformed) body mass and latitude of natural origin across species in the whole dataset or among African species (Table 1). For non-African species, the relationship was not significant using OLS, but was significant when phylogenetic relationships were accounted for (Table 1); in other words, although the overall relationship was not significant when assuming that all datapoints are independent (OLS), there is an increase in body mass with increasing latitude within clusters of more closely related species (among non-African ruminants)—which corresponds to the predictions made by Bergmann's rule (see Section IV.1).

Sexual size dimorphism increased with increasing body mass in the overall dataset and among non-African species (Table 1), corresponding to Rensch's rule (see Section IV.1). By contrast, the relationship was not significant using PGLS in African species (Table 1), indicating that the relationship does not occur equally in different taxonomic groups. Body mass was positively related to the percentage of grass in the natural diet in the overall dataset and among non-African species, but not among African species when accounting for phylogeny (Table 1). Accounting for phylogeny, an increase of sexual size dimorphism tended ($P = 0.053$) to occur with increasing latitude in the overall dataset but not in the African and non-African subsets (Table 1). Latitude was not correlated to the percentage of grass in the natural diet, but correlated negatively with the length of the gestation period in the overall dataset and among African species in OLS; using PGLS, there was a corresponding trend ($P = 0.056$) in the overall dataset (Table 1). The percentage of grass in the natural diet increased with increasing sexual size dimorphism in the overall dataset and among non-African species, but not among African species (Table 1).

The allometric equations for the length of the gestation period (Gestlength), determined using log-transformed data, were, with 95% confidence intervals in parentheses,

OLS: Gestlength (days) $= 131\,(117–146)\,\mathrm{BM}^{0.12(0.09–0.14)}$ ($R = 0.67$, $P < 0.001$)

PGLS: Gestlength (days) $= 145\,(120–174)\,\mathrm{BM}^{0.10(0.08–0.12)}$ ($R = 0.61$, $P < 0.001$).

Table 1. Correlations between the continuous measurements in the basic ruminant dataset used in this study (data from online Appendix S1)

		All species ($N = 110$)		African species ($N = 47$)		Non-African species ($N = 63$)	
Correlation	Model	R	P	R	P	R	P
BM—Lat	OLS	0.07	0.444	−0.08	0.603	0.16	0.203
	PGLS	0.12	0.213	−0.14	0.336	0.27	0.032
BM - BM m/f	OLS	0.42	<0.001	0.33	0.024	0.50	<0.001
	PGLS	0.36	<0.001	0.12	0.407	0.45	<0.001
BM - %grass	OLS	0.38	<0.001	0.29	0.047	0.47	<0.001
	PGLS	0.20	0.039	0.21	0.157	0.27	0.032
Lat - BM m/f	OLS	0.27	0.004	0.27	0.070	0.17	0.185
	PGLS	0.19	0.053	0.24	0.100	0.21	0.103
Lat - %grass	OLS	0.09	0.334	0.27	0.066	0.06	0.647
	PGLS	0.05	0.635	0.22	0.145	0.01	0.912
Lat - Gestlength	OLS	−0.25	0.007	−0.33	0.024	−0.14	0.273
	PGLS	−0.18	0.056	−0.27	0.065	−0.01	0.912
%grass - BM m/f	OLS	0.34	<0.001	0.13	0.383	0.56	<0.001
	PGLS	0.35	<0.001	0.15	0.312	0.49	<0.001

%grass, percentage of grass in the natural diet; BM m/f, body mass ratio between males and females (a measure for sexual size dimorphism); BM, body mass (log-transformed); Gestlength, length of gestation period; Lat, latitude of natural origin; OLS, ordinary least squares; PGLS, phylogenetic generalized least squares (accounting for phylogenetic relationships between species; differences to OLS indicated by grey shading).

(2) Quantifying seasonality

The correlation of the ordinal birth season categories with the continuous variables BPB50, 70, 80 and 90 in our data was significant ($P < 0.001$ in all cases), indicating that the quantitative approach of the BPB and the categorical approach necessary to classify literature data yields comparable results. All BPB variables showed a bimodal distribution across species; the larger the BPB chosen (from 50 to 90), the more this distribution was shifted to the right (Fig. 4). This bimodality suggests that although intermediate forms of reproductive seasonality exist, both strict seasonality and distinct aseasonality are the most common modes in ruminants. The smallest BPB50 was 10 days, the smallest BPB70 20 days, the smallest BPB80 30 days, and the smallest BPB90 40 days. Whereas the beginning of the birthing season in captivity did not show a systematic pattern in species originating from lower latitudes, the beginning of birthing seasons was similar for species originating from higher latitudes (Fig. 5).

(3) Comparison among ruminant groups

There were significant differences both in the mean latitude of origin and the degree of seasonality among ruminant taxonomic groups (Table 2). In particular, the extant Capreolinae (New World cervids) and the Caprinae originate from higher latitudes than many other ruminant taxa, and also have shorter BPBs. When correlating the minimum and maximum latitude of origin and BPB80 with the variance of the respective measurements for the taxonomic groups, a distinct pattern is evident: whereas the minimum latitude and the maximum BPB80 were not correlated with the variance of their respective measurements

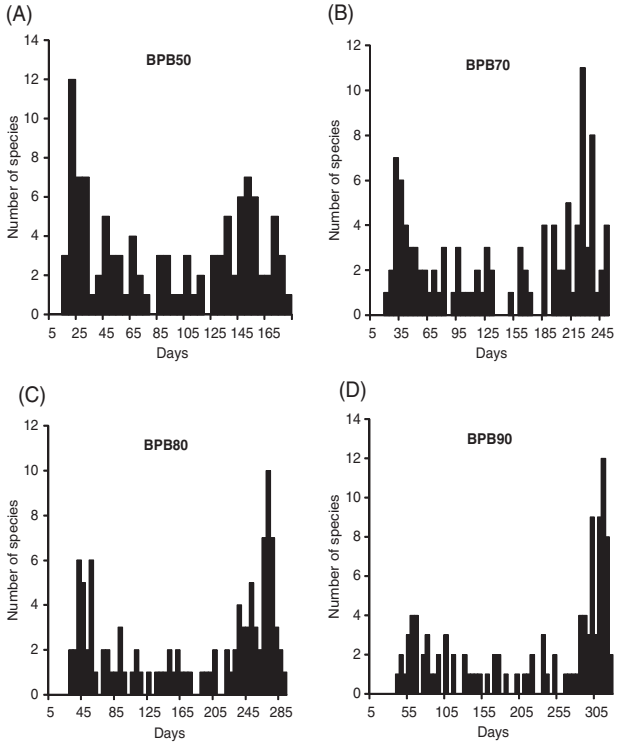

Fig. 4. Distribution of species according to their reproductive seasonality, characterised by the birth peak breadth (BPB, in days) in which (A) 50%, (B) 70%, (C) 80%, (D) 90% of all births occur.

(latitude: $r = 0.33, P = 0.290$; BPB80: $r = 0.10, P = 0.760$), the maximum latitude and the minimum BPB80 were both highly correlated (latitude: $r = 0.89$, $P < 0.001$; BPB80: $r = -0.85$, $P = 0.001$; Fig. 6), indicating that low-latitude origin and a low degree of reproductive seasonality did not

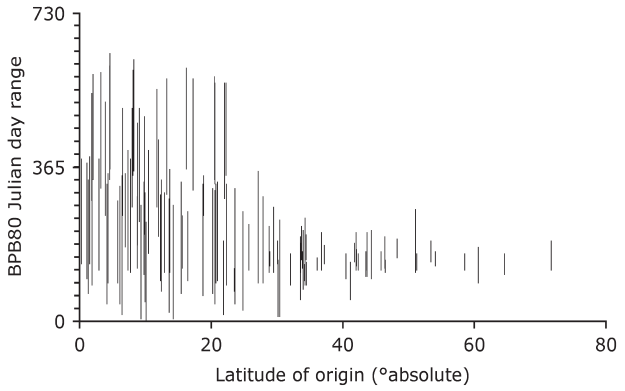

Fig. 5. Relationship between the (absolute) median latitude of origin of 110 ruminant species and the range of Julian days during which 80% of all births occur in captivity (BPB80). Note that for some more tropical species BPB80 reaches from one year to the next (crossing Julian day 365). For species from higher latitudes, the time of the birth window has a comparatively consistent start, and the birth window is shorter.

increase the overall range of these parameters covered by a taxonomic group, but that it was the inclusion of higher latitude origins and more distinct reproductive seasonality that increases the overall range of latitudes and seasonality present in a taxonomic group.

(4) Factors associated with seasonality

In the following, results for the BPB80 are given. Results for other BPBs are only reported if they deviate from those of BPB80.

The BPB80 was highly related to the latitude of geographic origin in the overall dataset, and among African and non-African species (Table 3). When plotting species on the world map according to their seasonality category, the relationship with latitude is evident (Fig. 7). Body mass was not correlated to any BPB (data not shown) and did not contribute significantly to the relationship between latitude and BPB80 (Table 4).

With respect to an influence of the mother-young-relationship on the effect of latitude on the BPB, there was a remarkable difference between the overall dataset and the non-African species on the one hand, with no additional effect of the hider/follower dichotomy, and the African species on the other hand (Table 5). In the African species, the hider/follower dichotomy had a significant effect on the BPB80, and in the PGLS model the inclusion of the hider/follower dichotomy reduced the effect of latitude on BPB80 to non-significance (Table 5).

The percentage of grass in the natural diet had no influence on the relationship between latitude and BPB80, neither in the overall dataset, nor among the African or non-African species, respectively (Table 6).

The effect of the mating system was tested in two different ways—using the mating-system categories 'monogamous', 'tending' and 'harem' as cofactors, or using the ratio of male to female body mass, which indicates the sexual size dimorphism, as a continuous covariable. For BPB80, mating system did not have a significant effect (data not shown), but for BPB50, an additional effect of mating system was significant in the overall dataset (Fig. 8); this significance was more pronounced with PGLS, indicating that the effect occurred in several ruminant lineages (Table 7). Sexual size dimorphism tended to have an effect on the relationship of latitude and the BPB80 in all datasets (Table 7).

For the overall dataset and the non-African species, the final model after backwards removal of non-significant factors resulted in only latitude having a significant effect on BPB80 (Table 3); for the African species, this procedure resulted in the model that included latitude and mother-young-relationship (Table 5).

Table 2. Mean ± standard deviation (range in parentheses) of the latitude of origin and the birth peak breadth in which 80% of all births occur (BPB80, in days) in wild ruminant species sorted according to taxonomic groups

Taxon	*N*	Latitude	BPB80
Tragulidae	2	6 (4–7)^{ab}	285 (285–285)^{ab}
Antilocapridae	1	37	45
Giraffidae	2	3 (2–5)^{a}	265 (255–275)^{ab}
Moschidae	1	53	50
Capreolinae	9	38 ± 19 (10–65)^{bc}	90 ± 80 (35–280)^{c}
Cervinae	13	26 ± 13 (7–48)^{ac}	145 ± 85 (45–270)^{ac}
Muntiacinae	3	22 ± 9 (12–28)^{ac}	250 ± 40 (205–280)^{ab}
Cephalophinae	4	6 ± 6 (1–12)^{a}	265 ± 10 (255–275)^{b}
Bovinae	18	16 ± 14 (1–51)^{a}	230 ± 50 (115–290)^{b}
Reduncinae	5	9 ± 4 (6–14)^{a}	255 ± 30 (205–280)^{ab}
Aepycerotinae	1	13	190
Antilopinae	18	16 ± 12 (0–46)^{a}	230 ± 70 (30–275)^{b}
Hippotraginae	6	14 ± 7 (5–21)^{a}	255 ± 15 (240–270)^{b}
Alcelaphinae	5	19 ± 10 (6–30)^{ac}	150 ± 35 (110–195)^{bc}
Caprinae	22	39 ± 13 (10–72)^{c}	80 ± 55 (30–260)^{c}

Means with different superscripts within a column differ significantly (ANOVA, Sidak *post hoc* test).

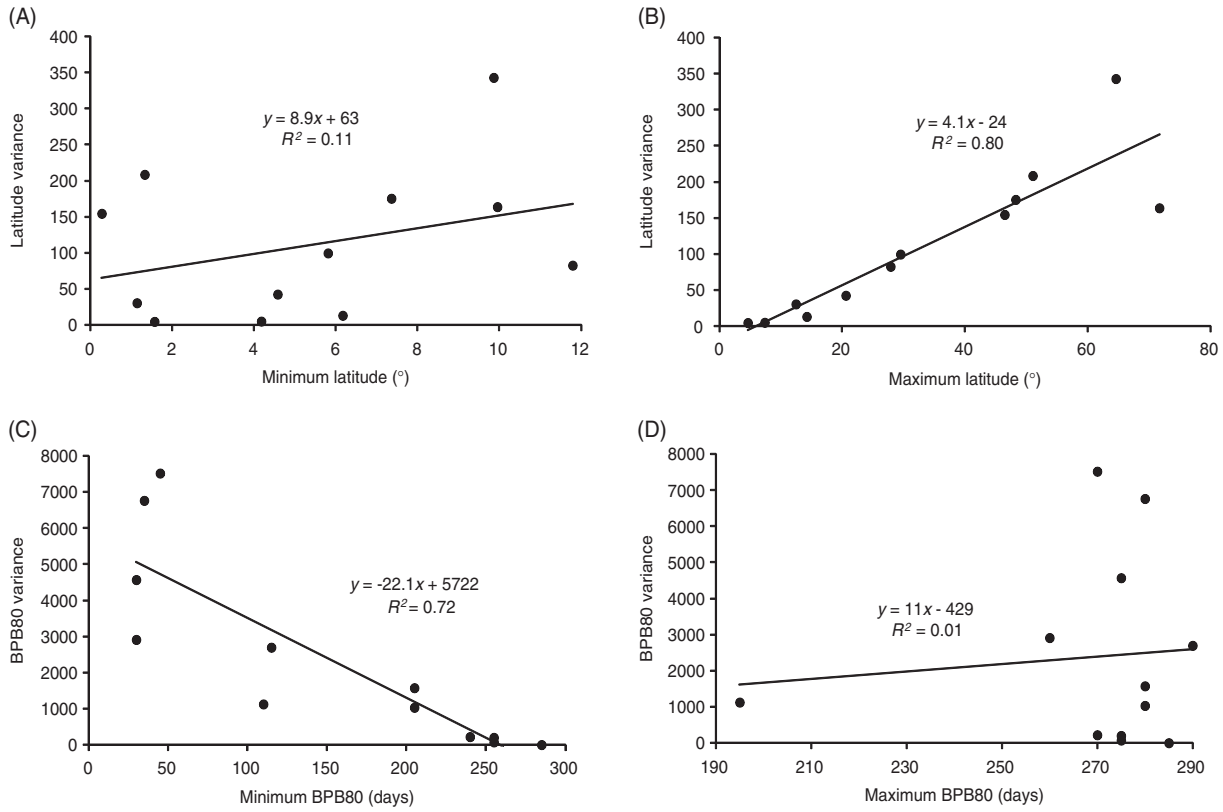

Fig. 6. Relationship between the (A) minimum and (B) maximum latitude of origin and the (C) minimum and (D) maximum of the birth peak breadth in which 80% of all births occurred (BPB80) with the variance of the respective measurements (data from Table 2) for different ruminant taxonomic groups. Note the clear pattern that among taxonomic groups, the variance in latitude increases with maximum latitude, and the variance in BPB80 is higher for lower minimum BPB80, suggesting that taxonomic groups expanded into higher latitudes, and evolved shorter BPB80, from lower latitudes (with longer BPB80).

Table 3. Correlations of the birth peak breadth in which 80% of all births occur (in days) and latitude of geographic origin in the complete dataset ($N = 110$ species), the African ($N = 47$) and the non-African species ($N = 63$) using ordinary least squares (OLS) and phylogenetic generalized least squares (PGLS)

Dataset	Model	*R*	*P*
All species	OLS	−0.82	<0.001
	PGLS	−0.78	<0.001
African species	OLS	−0.52	<0.001
	PGLS	−0.34	0.020
Non-African species	OLS	−0.79	<0.001
	PGLS	−0.75	<0.001

(5) Differences between captivity and the wild

Eleven out of 103 species (10.7%) changed their pattern of reproductive seasonality between the wild and captivity by more than one category. These were (category free ranging/captive) *Axis porcinus* (2/4), *Cervus alfredi* (2/4), *Cervus unicolor* (2/4), *Bos javanicus* (2/4), *Bubalus bubalis* (2/4), *Kobus megaceros* (2/4), *Antidorcas marsupialis* (4/2), *Antilope cervicapra* (2/4), *Gazella dorcas* (2/4), *Hippotragus niger* (2/4), and *Hemitragus hylocrius* (2/5). Ten of these changed to a less seasonal pattern in captivity; only the springbok (*Antidorcas marsupialis*) had a more seasonal pattern in zoos. All these species had their median origin at latitudes ≤23°, indicating that substantial changes in the seasonal pattern of reproduction occurred in low-latitude species only.

The only two seasonal species from the southern hemisphere for which exact data from the wild are available - *Damaliscus lunatus* and *Connochaetes gnou* - shifted their birth season start by nearly half a year (start of BPB80: 155 days earlier than data from the wild in both cases).

Comparing the beginning of the mating/conception season in free-ranging and captive populations of clearly seasonal (BPB80 < 33 days) species (data for captive species from online Appendix S1, for free-ranging populations from online Appendix S2; $N = 28$), there was a significant correlation between day length on the day reproductive activity was initiated in the wild and in captivity (Fig. 9). The slope of the linear regression line included 1.0 in the 95% confidence interval for the whole dataset in the PGLS analysis, and after excluding five visible outliers in both the OLS and the PGLS analysis (Table 8), indicating that the day lengths at the beginning of reproductive activity in the wild and in captivity were mostly identical, and that the shifts in the start of reproductive activity exemplified in Fig. 1 actually occurred (Fig. 10). The numerically positive intercept of the regression equation was not significantly different from zero (Table 8). Among the species considered outliers (see Fig. 9)

Fig. 7. Distribution of ruminant species across the world. Location of dots indicates the median of the natural origin; grey shading codes categorical seasonality. The degree of grey shading of dots (from white to black) correlates negatively with the length of the birth peak breadth in which 80% of all births occur (BPB80, in days), i.e. aseasonal species are represented by white dots (BPB80 = 240–290 days), strictly seasonal species by black dots (BPB80 = 30–80 days), with three intermediate shading steps (covering the BPB80 ranges of 180–235 days, 135–175 days and 85–125 days, respectively).

Table 4. Results from linear models testing for an additional effect of (log-transformed) body mass on the relationship between latitude of geographical origin and the birth peak breadth in which 80% of all births occur (in days) in the complete dataset ($N = 110$ species), the African ($N = 47$) and the non-African species ($N = 63$) using ordinary least squares (OLS) and phylogenetic generalized least squares (PGLS)

			Latitude		Body mass	
Dataset	Model	R^2	F/t	P	F/t	P
All species	OLS	0.68	222.248	<0.001	0.199	0.656
	PGLS	0.55	11.143	<0.001	0.227	0.821
African species	OLS	0.31	17.749	<0.001	2.642	0.111
	PGLS	0.12	2.500	0.016	0.300	0.765
Non-African species	OLS	0.63	99.073	<0.001	0.525	0.472
	PGLS	0.57	8.700	<0.001	0.704	0.484

Table 5. Results from linear models testing for an additional effect of the mother-young-relationship (hider/follower) on the relationship between latitude of geographical origin and the birth peak breadth in which 80% of all births occur (in days) in the complete dataset ($N = 110$ species), the African ($N = 47$) and the non-African species ($N = 63$) using ordinary least squares (OLS) and phylogenetic generalized least squares (PGLS; differences to OLS indicated by grey shading)

			Latitude		Hider/follower	
Dataset	Model	R^2	F/t	P	F/t	P
All species	OLS	0.68	157.416	<0.001	2.072	0.153
	PGLS	0.56	10.857	<0.001	0.968	0.335
African species	OLS	0.52	4.129	0.048	23.296	<0.001
	PGLS	0.42	1.733	0.090	4.049	<0.001
Non-African species	OLS	0.62	88.229	<0.001	0.029	0.865
	PGLS	0.75	8.600	<0.001	0.235	0.815

were the muskoxen (*Ovibos moschatus*), the bighorn sheep (*Ovis canadensis*) and the Dall sheep (*Ovis dalli*), whose populations start breeding at day lengths in the wild (19.9, 8.7 and 8.4 h, respectively) that are never achieved at the average latitude of the zoological institutions in our dataset (45° north). When kept at a higher latitude (than the origin), the onset of the mating season is delayed in some species, leading to later births, and when kept at lower latitude (than the origin), the onset of the mating season is earlier in some species, leading to earlier births. In the goitered gazelle (*Gazella subgutturosa*), for which data were available from Arabian and European zoological facilities, a corresponding shift in the birthing season was evident between the two captive populations (Fig. 11).

(6) Seasonality and gestation period

The relative gestation period showed a positive correlation with BPB in both OLS and PGLS, indicating that more seasonal species had shorter gestation periods (BPB80: OLS $\rho = 0.49$, $P < 0.001$; PGLS: $r = 0.36$, $P < 0.001$). For the absolute length of the gestation period, body mass, BPB80, the mother-young-relationship and sexual dimorphism (but not whether species were of African or non-African origin) were significant influence factors in OLS in the whole dataset. In PGLS, only body mass, BPB80 and sexual size dimorphism were significant (Table 9). For African species, body mass and BPB80 were the only significant covariables in PGLS (Table 9). Among non-African species, the inclusion or exclusion of the roe deer (*Capreolus capreolus*)—known to

Table 6. Results from linear models testing for an additional effect of the percentage of grass in the natural diet on the relationship between latitude of geographical origin and the birth peak breadth in which 80% of all births occur (in days) in the complete dataset ($N = 110$ species), the African ($N = 47$) and the non-African species ($N = 63$) using ordinary least squares (OLS) and phylogenetic generalized least squares (PGLS)

			Latitude		%grass	
Dataset	Model	R^2	F/t	P	F/t	P
All species	OLS	0.68	221.582	<0.001	1.244	0.267
	PGLS	0.55	11.000	<0.001	1.250	0.214
African species	OLS	0.28	12.907	0.001	1.146	0.290
	PGLS	0.12	2.500	0.016	0.500	0.620
Non-African species	OLS	0.63	98.737	<0.001	1.101	0.298
	PGLS	0.76	8.600	<0.001	1.000	0.321

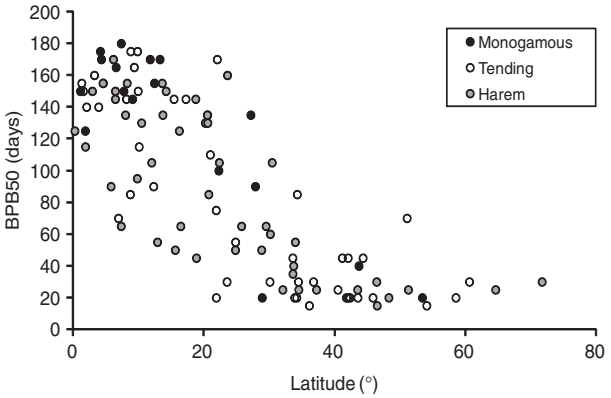

Fig. 8. Relationship between birth peak breadth in which 50% of all births occur in captivity (BPB50, in days) and the latitude of a species' origin. Note that species from higher latitudes demonstrate a higher degree of reproductive seasonality when compared to species that originated from lower latitudes.

have delayed implantation and therefore a particularly long gestation period—had a distinct effect on the results of the analyses (Table 9). Without the roe deer, BPB80 was the only significant factor influencing the gestation period in addition to body mass in PGLS; when the roe deer was included, however, the influence of BPB80 was not significant in PGLS, whereas now that of the mother-young-relationship as well as that of sexual dimorphism was. Generally, the interaction between body mass and BPB80 was not significant (not shown), indicating no evidence for a change of the influence of BPB80 across the body size range. Ruminants with a more distinct seasonal reproduction had, on average, shorter gestation periods than similar-sized less-seasonal ruminants (Fig. 12A); in other words, species with a more pronounced seasonal reproduction pattern often had relatively short gestation periods for their body mass. This pattern was evident in several ruminant lineages (Fig. 12B, C). There were some notable outliers to this pattern. Giraffids have longer gestation periods than other ruminants (Fig. 12A, B; Müller *et al.*, 2011*b*). The roe deer (*Capreolus capreolus*) had a surprisingly long gestation period for a seasonal (and for any) ruminant of its body size. The pronghorn (*Antilocapra americana*), the pudu (*Pudu puda*), and the Père David's deer (*Elaphurus davidianus*) also had relatively long gestation periods for ruminants of their body size range with a distinct seasonal reproduction pattern (Fig. 12A, B).

IV. DISCUSSION

This study demonstrates that in contrast to warning against the use of data from captive populations for the characterisation of the seasonality of reproductive events—because they differ from those in the wild (Fairall, 1968), such data can be used fruitfully, partly even *because* of a systematic difference to events in free-ranging populations. The degree of reproductive seasonality of a species can be characterised by a continuous parameter, the birth peak breadth (BPB, the number of days in which a certain percentage of all births occur). This parameter correlates well with the more traditional categorical description of seasonality (highly seasonal, seasonal, aseasonal) and facilitates testing the influence of biological and environmental factors on the degree of seasonality. In particular, we could demonstrate that seasonality of reproduction in ruminants is independent of body mass and mainly linked to the latitude of the origin of the species; that there is a difference between African and non-African species with respect to birth synchrony in the hider/follower strategy; that the photoperiodic signal that many seasonal species adapt to is probably the absolute day length; and that a shortening of the gestation period may be an important adaptation of many

Table 7. Results from linear models testing for an additional effect of the mating system (monogamous/tending/harem) or the sexual size dimorphism on the relationship between latitude of geographical origin and the birth peak breadth (in days) in which 50% (mating system) or 80% (dimorphism) of all births occurred in the complete dataset ($N = 110$ species), the African ($N = 47$) and the non-African species ($N = 63$) using ordinary least squares (OLS) and phylogenetic generalized least squares (PGLS; differences to OLS indicated by grey shading)

			Latitude		Mating system	
Dataset	Model	R^2	F/t	P	F/t	P
All species	OLS	0.65	173.633	<0.001	3.156	0.047
	PGLS	0.55	11.750	<0.001	4.140	0.019
African species	OLS	0.30	11.429	0.002	1.465	0.242
	PGLS	0.18	2.083	0.043	1.800	0.177
Non-African species	OLS	0.64	93.096	<0.001	1.874	0.163
	PGLS	0.78	10.000	<0.001	2.180	0.122
					Dimorphism	
All species	OLS	0.70	199.876	<0.001	6.456	0.012
	PGLS	0.58	11.000	<0.001	1.886	0.062
African species	OLS	0.32	12.214	0.001	3.251	0.078
	PGLS	0.19	1.929	0.060	2.054	0.046
Non-African species	OLS	0.64	95.263	<0.001	3.874	0.054
	PGLS	0.60	8.300	<0.001	1.748	0.086

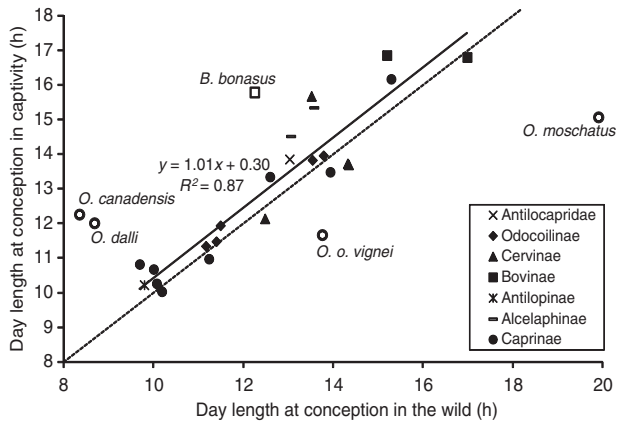

Fig. 9. Relationship between the day length at the beginning of mating/conception in the wild and in captivity (data from online Appendices S1 and S2) in 28 ruminant species. When omitting five outlier species (indicated by open symbols) from the analysis, a linear relationship results (solid line) that is not significantly different from the $y = x$ line (broken line) (for statistics, see Table 8).

seasonal species to ensure birthing at times of favourable conditions but facilitating a rutting season to take place in autumn or even early winter at the same time. In particular, this study ($N = 110$) increases the species number included in comparative analyses on the relevance of seasonal reproduction patterns significantly (Rutberg, 1987: $N = 27$; Kiltie, 1988: $N = 28$ ruminant species), and thus allows a more rigorous testing of additional effects, such as mother-young relationship, diet, or mating type. Our basic data compilation also demonstrated some additional relationships between life-history and ecological variables among ruminants.

(1) General characteristics of ruminant species

Bergmann's rule states that in individuals of a species, or of closely related species, body mass increases with increasing latitude. Previous analyses of ruminant species did not demonstrate such a relationship on an interspecific level (Bro-Jørgensen, 2008), even though intraspecific analyses confirmed the pattern (Ashton, Tracy & de Queiroz, 2000; Meiri & Dayan, 2003). Our analyses revealed that Bergmann's rule also applies to ruminants, if one focuses on non-African species only (i.e. mostly non-tropical species), and only if the phylogenetic relationships between the species are considered. This finding represents one of the rarer cases where a nonsignificant finding in ordinary regression analysis becomes significant when phylogenetic relationships are accounted for (*cf.* fig. 1, p. 147 in Baker, 2002; Müller *et al.*, 2011*a*). Although testing of Bergmann's rule was not a primary aim of the present study, this analysis represents an exquisite example of why controlling for phylogeny in comparative analyses is highly relevant.

Another ecological rule, Rensch's rule (Abouheif & Fairbairn, 1997), indicating that the degree of sexual dimorphism among species increases with their mean body mass, was also confirmed in the present study. This rule had been confirmed previously for wild (Weckerly, 1998; but see Bro-Jørgensen, 2008) and domestic ruminants (Polák & Frynta, 2009, 2010), but not among the larger group of ungulates (Alexander *et al.*, 1979; Abouheif & Fairbairn, 1997), emphasizing the importance of testing patterns at various levels of taxonomy (Clauss, Kaiser & Hummel, 2008). The relationship between latitude and sexual dimorphism, such as postulated by Geist (hypothesis 10 in Geist, 1974*b*) or Isaac (2005), only tended towards significance in the overall dataset when accounting for phylogeny, and was not evident in the African or non-African subsamples (Table 1). Geist (1974*b*) himself provided several exceptions to his hypothesis. Elucidating reasons for sexual dimorphism in ruminants will require more variables than provided in our study.

Conflicting results have been generated on a general increase in the proportion of grass in the natural diet with body mass in various studies, and results may well depend on the selection of species at hand (reviewed in Clauss *et al.*, 2008). The finding that the relationship was not significant considering phylogenetic relationships among African species supports the concept that the African biome requires, because its C4 grasses are different from other forages on a global level, particular adaptations in grazing species (Codron *et al.*, 2008*b*; Codron & Clauss, 2010); these adaptations are not restricted to body mass alone and may be reflected in phylogenetic lineages. Sexual size dimorphism has been related to the type of habitat (closed/open), with dimorphic species usually occurring in more open habitats (Bro-Jørgensen, 2008). Open habitats are also generally associated with

Table 8. Linear regression analysis (in ordinary least squares, OLS, and phylogenetic generalized least squares, PGLS; differences to OLS indicated by grey shading) according to $y = a + bx$ with the day length at conception in captivity as the dependent variable, and the day length at conception in the wild as the independent variable (for species selection, see online Appendix S2)

	OLS			PGLS		
	a	*b*	R^2	*a*	*b*	R^2
All species ($N = 28$)	5.37 (2.56; 8.18)	0.62 (0.40; 0.83)	0.56	0.43 (−3.74; 4.60)	0.93 (0.62; 1.24)	0.56
Without five outliers ($N = 23$)	0.30 (−1.98; 2.58)	1.01 (0.83; 1.19)	0.87	1.37 (−0.55; 3.29)	0.86 (0.72; 1.00)	0.87

Results are given with 95% confidence intervals in parentheses. See Fig. 9 for the pattern of the original data and the identification of outliers.

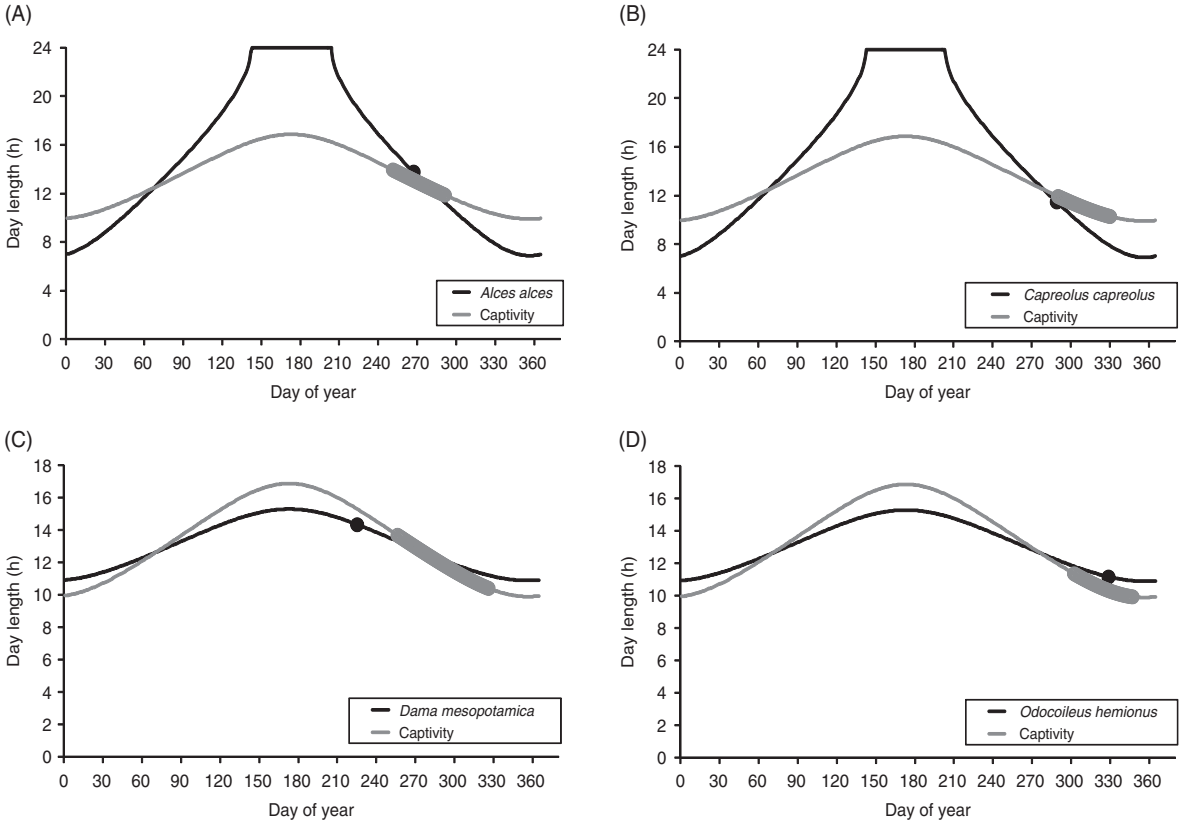

Fig. 10. Comparison of the day length (including civil twilight) at different days of the year at the average latitude of the zoological institutions of this study (captivity, 45° north), and the latitude of the free-ranging populations of (A) moose (*Alces alces*), (B) roe deer (*Capreolus capreolus*), (C) Mesopotamic fallow deer (*Dama mesopotamica*), and (D) mule deer (*Odocoileus heminous*). The beginning of reproductive activity in the wild (data from online Appendix S2) is indicated by the black dot; the time period in which 80% of all offspring are conceived in captivity is indicated by the grey circles. Note that the different cases of time shifts between the wild and captivity as exemplified in Fig. 1 actually occur.

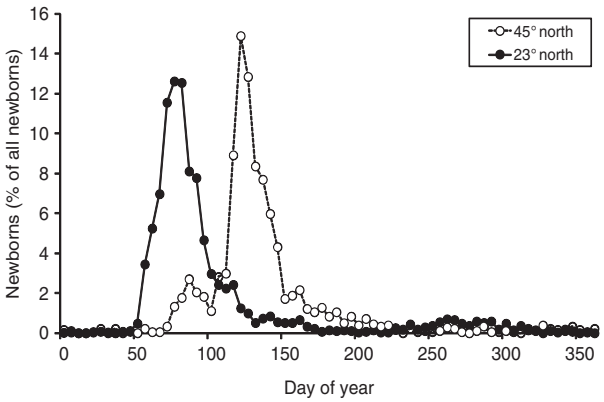

Fig. 11. Proportion of births (in % of all births) in two populations of goitered gazelles (*Gazella subgutturosa*) kept at a latitude of approximately 23° (Arabia) and 45° north (data used herein). Note the earlier birth peak in the population kept at lower latitude.

grazing (Pérez-Barberìa,Gordon & Nores, 2001). The relationship between % grass and body mass and dimorphism might therefore reflect a habitat influence (Pérez-Barberìa, Gordon & Pagel, 2002) rather than an influence of the feeding niche itself—in other words, % grass might just represent a proxy for habitat when tested against body mass. The fact that there is no relationship between % grass and sexual dimorphism among African species suggests the interpretation that in the African biome, the browser/grazer spectrum might not be as distinctively distributed between habitats, with several savannah-based browsers and mixed feeders, and/or that in the African biome, an adaptation to grazing itself (rather than to habitat characteristics for which grazing is a proxy) may be more relevant due to the special nature of C4 grasses as mentioned above.

(2) Quantifying seasonality

In this study, we expressed the degree of seasonality as the number of succeeding 5-day intervals within a year where a certain percentage (i.e. 50, 70, 80 or 90%) of all births took place. Many previous studies did not apply a quantitative measure to the degree of reproductive seasonality, despite using quantitative data and statistical tests to allocate species to seasonality categories (Pelt, 1967). Variations in the percentages of required births result in different extents of these birth-windows (from 2 months for BPB50 up to 11 months for BPB90). The correlation between these BPB and the more traditional seasonality categories did not indicate that a certain BPB was more suited for

Table 9. Results from general linear models (retaining only variables/factors significant using original least squares, OLS) testing for the effect of reproductive seasonality (measured as the birth peak breadth in which 80% of all births occurred, BPB80), the mother-young relationship (hider/follower) or the sexual size dimorphism on the relationship between body mass and the length of the gestation period in the complete dataset ($N = 110$ species), the African ($N = 47$) and the non-African species ($N = 63$) using OLS and phylogenetic generalized least squares (PGLS; differences to OLS indicated by grey shading)

	Model	R^2	Body mass	BPB80	Hider/follower	Dimorphism
All species	OLS	0.68	$F = 200.723$ $P < 0.001$	$F = 5.035$ $P = 0.027$	$F = 10.322$ $P = 0.002$	$F = 22.877$ $P < 0.001$
	PGLS	0.50	$t = 11.000$ $P < 0.001$	$t = 3.667$ $P < 0.001$	$t = 1.000$ $P = 0.320$	$t = 2.000$ $P = 0.048$
African species	OLS	0.72	$F = 105.064$ $P < 0.001$	$F = 6.265$ $P = 0.016$	—	$F = 10.637$ $P = 0.002$
	PGLS	0.55	$t = 6.000$ $P < 0.001$	$t = 2.556$ $P = 0.014$	—	$t = 1.000$ $P = 0.323$
Non-African species	OLS	0.66	$F = 100.298$ $P < 0.001$	$F = 4.086$ $P = 0.048$	$F = 14.222$ $P < 0.001$	$F = 9.276$ $P = 0.003$
	PGLS	0.51	$t = 7.437$ $P < 0.001$	$t = 1.524$ $P = 0.133$	$t = 2.097$ $P = 0.040$	$t = 2.111$ $P = 0.039$
Non-African species (without roe deer)	OLS	0.73	$F = 129.629$ $P < 0.001$	$F = 9.018$ $P = 0.004$	$F = 15.030$ $P < 0.001$	$F = 8.843$ $P = 0.004$
	PGLS	0.59	$t = 8.399$ $P < 0.001$	$t = 2.188$ $P = 0.033$	$t = 0.954$ $P = 0.344$	$t = 1.703$ $P = 0.094$

the description of seasonality than another. Caughley & Caughley (1974) used a nonlinear regression equation to describe the birth pattern of free-ranging impala (*Aepyceros melampus*) and estimated the peak of the birth season as the median date of births (explicitly assuming a normal distribution of births around this time point). Because of the non-symmetric appearance of many birth distribution patterns (see Fig. 2), the standard deviation used in their study to describe the duration of the birthing season does not necessarily describe the real birth season very precisely. Similarly, the calculation of the quantitative reproductive asynchrony index (RAI) introduced by Kiltie (1988), or the approach of Ogutu *et al.* (2010) to describe the birth peak and the degree of birth synchrony by fitting Poisson regression models, are based on the assumption of a normal distribution around a birth peak. By contrast, the BPB, with its approach to find the smallest number of 5-day intervals in which a certain percentage of all births occurred (possible because of the high resolution of observations in captivity that are made on a daily, not a monthly basis) achieves a higher level of precision in describing the peak birth season. Rutberg (1987) and Meng *et al.* (2003) defined the birth season of a species as number of consecutive days during which 75–80% of the year's offspring are born, beginning from the first birth event that was observed in that year until 75 or 80% were achieved. Note the better representation of the real reproductive pattern of the BPB-approach (Fig. 3), because the BPB is not linked to the first birth event of the year but to the time period with the most concentrated number of birth events.

(3) Evolving seasonality

Rutberg (1987) found, using a nested analysis of variance, a high degree of variation in the birth season length in ruminant taxa, suggesting that this characteristic is subject to a high degree of adaptive selection. Analyses on a higher taxonomic level suggest that it was the expansion into higher latitudes, and the evolution of a more seasonal reproductive pattern, that led to an increase in the overall range covered by a taxonomic ruminant subgroup (Fig. 6). In agreement with these findings, Jabbour *et al.* (1997) suggest that deer evolved in subtropical climates, and that expansion into higher latitudes was accompanied by the evolution of seasonal reproduction, and by changes in body mass (Geist, 1987). Non-seasonal reproduction is thus considered the ancestral state, as supported by our analyses for all ruminants in general; note that this does not mean that seasonality cannot evolve in low latitudes. One factor supporting ruminant radiation into higher latitudes could be that, aside from the giraffids, their gestation periods are below 1 year and can be comparatively short (*cf.* the gestation period of domestic cattle at about 278 days compared with that of similar-sized domestic horses at about 340 days - Jafar, Chapman & Casida, 1950; Bos & Van der Mey, 1980), which makes an adaptation to seasonal environments feasible without loss of a vegetation period for the interbirth interval (Kiltie, 1988). As stated in Section I, the fact that species with gestation periods longer than a seasonal cycle live or lived at higher latitudes indicates that while a short gestation period may be an advantage at higher latitudes, it is not a precondition for expansion into such regions. It might be particularly interesting to investigate the climatic conditions, the geographic distribution and the competitive replacement of fossil giraffids (Solounias, 2007) in this respect—the only true ruminants with exceptionally long gestation periods.

The finding that New World deer (Capreolini) show a numerically higher reproductive seasonality than Old world deer (Cervini) corresponds to Jabbour *et al.*'s (1997) claim that

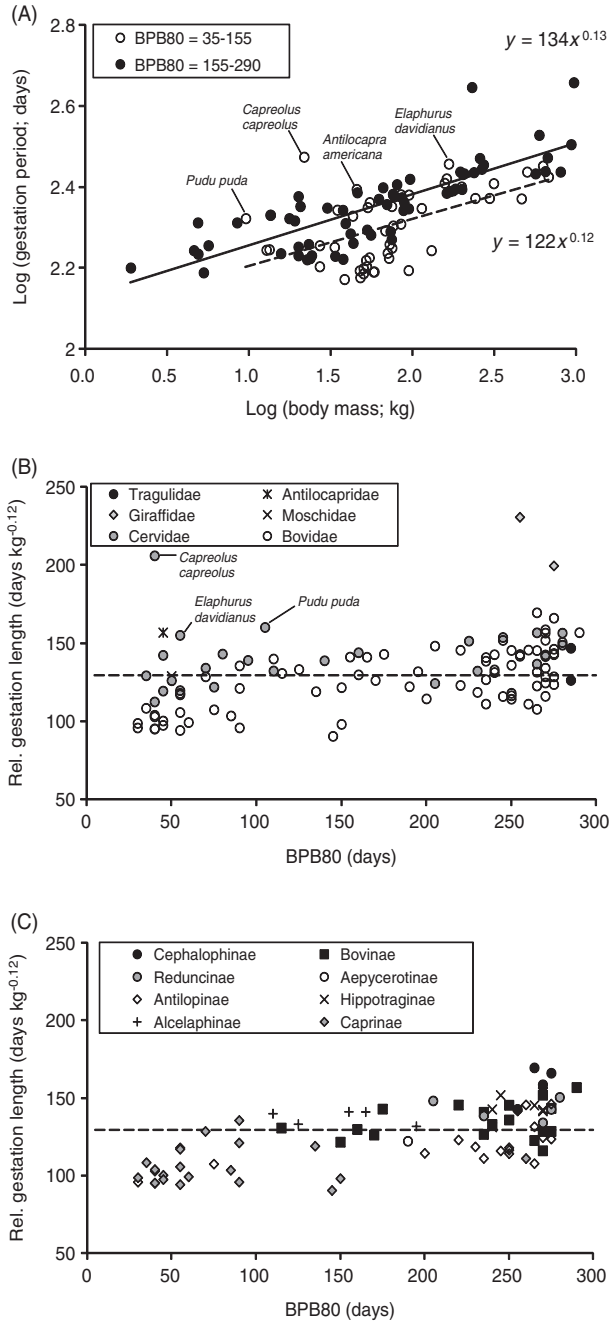

Fig. 12. Relationship between (A) body mass and the length of the gestation period for ruminant species of different seasonality classes [in terms of the length of the birth peak breadth in which 80% of all births occur (BPB80, in days); note that for statistical evaluation, BPB80 was used as a continuous measure—see Section III.6]; (B,C) the relationship of BPB80 and the relative length of the gestation period (per unit body mass$^{0.12}$) in ruminant groups (B) and bovid groups (C).

due to the historical high-latitude dispersal routes of New World deer, a seasonal reproduction might be considered the ancestral state, and that tropical New World deer should therefore express seasonal reproduction when kept at higher latitudes—something not necessarily to be expected for Old World deer. Notably, several Old World deer species were amongst those in which a less seasonal pattern was observed in captivity; however, no New World deer was amongst those considered 'changers', suggesting a more fixed reproductive seasonality. Nevertheless, the pampas deer (*Ozotoceros bezoarticus*), considered aseasonal in the wild (Jabbour *et al.*, 1997; category 4), had a more seasonal pattern in captivity (category 3; BPB80 < 33 days), which still corresponds to Jabbour *et al.*'s (1997) prediction.

The direction of day-length change separates the short-day (days shorter than the days before) and long-day (days longer than the days before) breeders. Ruminants are usually considered short-day breeders if seasonal, whereas many small mammals such as rodents or carnivores that conceive and give birth in the same year, and domestic horses with their longer gestation periods, are examples of long-day breeders (Sadleir, 1969; Bronson, 1989). There was only one seasonal long-day breeder in the current dataset - the Eld's deer (*Cervus eldi*), which is in accordance with published findings on ovarian function in this species (Monfort *et al.*, 1990). For the rusa deer (*Cervus timorensis*), long-day breeding has also been reported (Van Mourik & Stelmasiak, 1990), which is in accordance with our findings—but this species was not considered seasonal in our dataset due to its long BPB80 of 225 days. All the other seasonal species were short-day breeders. The exception of the Eld's (and rusa) deer suggests that short-day breeding need not necessarily be considered a plesiomorphic character in ruminants, but that different adjustments of breeding seasons can occur comparatively easily among closely related species. This is also demonstrated by the interesting difference between Himalayan tahr (*Hemitragus jemlahicus*) that are strictly seasonal both in captivity and the wild, and the Nilgiri tahr (*Hemitragus hyloricus*—'the world's most equatorial wild caprid') that are strictly seasonal in the wild but breed throughout the year in captivity (Rice, 1988; Paré *et al.*, 1996)—an impressive example for the potential for divergence in the adaptation to seasonally fluctuating environments in closely related species.

(4) Causative factors for seasonality: interspecific comparisons

(*a*) *Latitude*

This study confirms that on a global level, latitude is the most important factor influencing reproductive seasonality. The fact that the effect of the latitude of origin was hardly attenuated by management in captivity (which ensures a constant provision of dietary resources and a predator-free environment) gives evidence for a genetically fixed reproductive pattern that is triggered by factors other than nutritional status—most likely, by photoperiod (Bradshaw & Holzapfel, 2007). The reproductive periods (conception and birth) become shorter, i.e. ruminant species become more seasonal, with increasing latitude of geographic origin of the species (and not the animals' actual geographic position at the zoo). Our findings confirm previous qualitative and quantitative evaluations in this respect (Rutberg, 1987; Bronson, 1989; Santiago-Moreno *et al.*, 2006), with a much larger number of species.

With increasing latitude, spring starts later, but winter starts earlier in the year (Sparks & Menzel, 2002), shortening the time of favourable environmental conditions for the offspring. In Northern mammals, survival rates of newborns that are born late in the season are reduced, as they fail to accrue body reserves necessary to survive harsh winters (Clutton-Brock, Guinness & Albon, 1983; Rutberg, 1987; Festa-Bianchet, 1988; O'Donoghue & Boutin, 1995; Santiago-Moreno *et al.*, 2006). Thus, there is great selective pressure on early births and short birthing periods.

Fixed seasonal patterns of reproduction do not seem to evolve to the same extent in latitudes that have less drastic changes in resource availability and a higher degree of climatic unpredictability (tropics and sub-tropics). A possible explanation for a low proportion of seasonally reproducing species around the equator is that a limited reproductive period bears a potential threat for the development of a population. Unpredictable events, like droughts or unusual cold and wet meteorological conditions might eradicate the majority of the offspring of a whole reproductive cycle.

(*b*) *Altitude*

Although not tested in this study due to a lack of sufficient information, an additional factor that may influence the degree of reproductive seasonality is the altitude of a species' origin. Conditions at high altitudes are in many ways analogous to those at high latitudes, and it has been suggested that high-altitude habitats, such as Tibet, could have pre-adapted species to life at lower altitudes but higher latitudes (Deng *et al.*, 2011). As seasons of favourable conditions become shorter with increasing altitude, one can predict that species living at higher altitudes should show a higher degree of seasonality (Mooney & Billings, 1961; Sadleir, 1969; Körner, 2007), in addition to the seasonality due to their latitude of origin. Data on lambing periods from 30 populations of North American mountain sheep showed that the correlations between the start of the reproductive season and their duration with latitude are enhanced when latitude is replaced by a phenological index that additionally incorporates information on altitude (Bunnell, 1982). Differences in the birthing period between white-tailed deer (*Odocoileus virginianus*) and mule deer (*Odocoileus hemionus*) populations at similar latitudes, but at different altitudes, also suggests such an effect (Ransom, 1966; Bowyer, 1991). The generally short BPBs of species of the Caprinae subfamily—goats and sheep, which are usually alpine species—support this hypothesis (Table 2).

(*c*) *Predator avoidance*

In studies of seasonal reproduction of ruminants, the two major explanatory scenarios usually evoked are that of an adaptation to seasonally variable resources and that of predator avoidance (Rutberg, 1987 and many publications referring to him). As outlined in Section I, follower species should benefit from a high degree of birth synchrony, whereas hider species should benefit from asynchronous births (Ims, 1990*a*, *b*) to avoid predation.

Testing this concept by using the hider-follower dichotomy may be problematic in itself, because this dichotomy may not adequately reflect the real and potentially relevant range of behavioural adaptations across species, where for example the duration of the 'hider' stage, and the distance between mother and hidden neonate, may vary systematically (Ralls, Kranz & Lundrigan, 1986)—but a finer-scale classification of ruminant species across the hider-follower spectrum is lacking so far. Parallels in the characteristics of ungulates and macropods that correlate with the respective hider-follower strategies (Fisher, Blomberg & Owens, 2002) suggest that seasonality is not the major factor influencing the evolution of the mother-neonate relationship. Most importantly, however, the requirements of adaptation to seasonal resource availability might overrule the adaptive value of adjusting reproductive patterns to predation pressure.

Correspondingly, we did not detect an influence of the hider-follower dichotomy in the overall dataset, or in the non-African species (Table 5). Predation avoidance has been rejected as a cause for birth synchronicity in several wild ruminant species from higher latitudes (Rutberg, 1984; Festa-Bianchet, 1988; Rachlow & Bowyer, 1991; Green & Rothstein, 1993; Aanes & Andersen, 1996; Bowyer, Van Ballenberghe & Kie, 1998; Linnell & Andersen, 1998; Post *et al.*, 2003). Several of the temperate-zone ruminants are hider species yet show a distinct seasonal reproduction. Based on theoretical modelling, Ims (1990*a*) demonstrated that predator saturation due to birth synchrony could only work against highly specialized predators that do not switch prey species; against generalist predators (such as those preying on most hider species), the strategy is, by contrast, disadvantageous. Panzacchi *et al.* (2008) actually demonstrated such an increased predation of foxes (*Vulpes vulpes*) on roe deer fawns and concluded that birth synchrony could not have evolved primarily as an anti-predator strategy in this hider species. By contrast, Testa (2002) suggested that birth synchrony could also evolve in species susceptible to this kind of predation, because individuals born at the very beginning of a birthing period should have a higher chance of survival, due to a time lag between the very beginning of the birthing period and the reaction of predators to search for neonate prey. We conclude that even if effects of birth synchrony and timing of birth on predation risk can be demonstrated in temperate-zone ruminants (see Section I), these effects can only be considered of secondary importance at best for reproductive seasonality.

Notably, support for the anti-predation hypothesis derives from the African biome (Estes, 1976; Sinclair *et al.*, 2000*b*; see also Moe *et al.*, 2007, who consider the absence of reproductive seasonality as an anti-predator strategy in hider species). Among the African species, seasonal variability in available resources that can be directly linked to photoperiodism is less distinct, and therefore, the effect of predator avoidance on reproductive patterns might be more prominent. Our analysis supported the hypothesis that

those ruminants classified as followers show a higher degree of reproductive seasonality than those classified as hider species; including the effect of the hider-follower classification even led to nonsignificance in the latitude-BPB-relationship in PGLS (Table 5). Therefore, we must conclude that in the African ruminant guild, some species classified as followers show adaptations, putatively for predator swamping, that are genetically fixed (and most likely linked to photoperiodism) so that they are apparent even under captive conditions of permanent food supply and protection from predators. It is in particular in comparison to seasonal reproduction triggered by resource availability (see Section IV.5*b*), which is also prominent in tropical and sub-tropical regions, that the high relevance of predator avoidance for these few species must be emphasized. Yet we cannot discard the hypothesis that those African species classified as followers (*S. caffer*—the only species in this group classified as rather non-seasonal, *D. lunatus, D. pygarus*, *C. taurinus*, *C. gnou*, *C. nubiana*, *A. lervia*) share some other characteristics that favoured the evolution of photoperiod-linked reproductive seasonality, which would make the effect of the hider-follower dichotomy a spurious finding. Adaptation to altitude (in the Caprinae) and to photoperiod-linked seasonal rainfall and migration are possible alternative explanations in this respect. We conclude that, globally, birth synchrony should rather be understood as an adaptation to the seasonal availability of resources and not primarily as a predator-avoidance strategy in ruminants.

(*d*) *Natural diet*

Putative differences in the degree of seasonality between grazers and browsers due to a shorter flush period of grasses and the associated shorter time span of high-quality food to raise offspring when compared to browse are already controversial in the literature (Leuthold & Leuthold, 1975; Rutberg, 1987; Kiltie, 1988; Skinner *et al.*, 2002). There is no systematic effect of latitude on the occurrence of feeding types in ruminants (Table 1). In the temperate zone, seasonal variation in resource availability affects grazers and browsers alike. In the African biome, there was also no effect of feeding type, which we propose is due to the fact that at times of vegetation growth, not only grass but also browse forage is of higher nutritional value (Owen-Smith & Cooper, 1989; Meissner, Zacharias & O'Reagain, 1999).

(*e*) *Mating type*

Isaac (2005) hypothesized that latitude influenced the occurrence of sexual size dimorphism in mammals due to variations in seasonal food availability, which, under pronounced seasonal conditions, might favour the seasonal aggregation of animals and thus polygamous mating strategies. She suggested that studies that investigate sexual size dimorphism in mammals without accounting for the effect of latitude, seasonal variation or adaptations to seasonality might be 'fundamentally flawed'. There was a trend for a correlation between latitude and sexual size dimorphism in our dataset in PGLS (Table 1), and sexual size dimorphism and mating type did show some relationship with the degree of reproductive seasonality. On the one hand, the mating type of species had an influence on the degree of reproductive seasonality as assessed by BPB50 (i.e. only considering the highest birth peak), with polygamous species having smaller birth peaks for their latitude than monogamous species. On the other hand, sexual size dimorphism was always either marginally significant or close to significant as a covariable in the general linear models applied (Table 7). We suggest that mating type and dimorphism are characteristics that follow the degree of seasonality of ruminant species, rather than facilitate it. Monogamous males that live in close proximity to their (single) partner throughout the year do not have to cope with the problem of finding the female when it is in oestrus. By contrast, males of polygamous species attempt to copulate with as many females as possible, resulting in higher sexual competition amongst the males. Such a mating strategy can more easily evolve under conditions when most females are in oestrus at the same time (such as under seasonal conditions), limiting the time period of high reproductive investment for the males. Nevertheless, many polygamous species (e.g. members of the genera *Kobus*, *Hippotragus*, and *Gazella*) demonstrate an aseasonal mode of reproduction.

(5) Environmental correlates of seasonality: intraspecific comparisons

In general, the comparison of reproductive seasonality between captive and wild populations emphasizes the high relevance of the latitude of origin, and hence photoperiodism, and the comparatively low relevance of resource-induced seasonality in the whole ruminant dataset. In contrast to the expectation that a comparison of free-ranging and captive populations might reveal a high number of species that switch to a less distinct seasonality under constant resource provision in captivity (Clauss, Hume & Hummel, 2010), the number of such species was actually remarkably low.

(*a*) *Photoperiodism*

As there was only one species that changed from a clear seasonal pattern in the wild to a clear non-seasonal pattern (category 5) in captivity (*Hemitragus hyloricus*), it can be argued that such a complete reversal of reproductive seasonality is rarely possible. Consistent with this, the ancestors of the most important domestic ruminant—cattle (*Bos taurus, B. indicus*) originate from populations of wild aurochs (*B. primigenius*) (Beja-Pereira *et al.*, 2006), for which - according to the latitude where their domestication started (India) - a rather aseasonal reproductive behaviour can be proposed. In fact, a similar argument can be made for some non-ruminants as well, such as the domestic pig (*Sus scrofa domesticus*), which originated from populations of wild boar (*Sus scrofa*) initially in the Middle East (Giuffra *et al.*, 2000). By contrast, the ancestors of the more seasonal domestic goats (*Capra hircus*) and sheep (*Ovis aries*) had been domesticated in the highlands of the Middle East region with a more seasonal environment (Zeder & Hesse, 2000; Pedrosa *et al.*, 2005). Similarly, Ortavant

et al. (1985) stated that the original site of domestication determines the pattern of seasonal reproduction in domestic sheep as well as horse breeds.

The finding that the timing of seasonal reproduction is shifted by half a year if a species is kept at the hemisphere from which it does not originate, like *Damaliscus lunatus* and *Connochaetes gnou* in this study (and many similar observations referenced in Section I) is evidence for a general effect of day-length change on reproductive seasonality in ruminants. Further support for an effect of day-length change comes from the shift in the reproductive period with latitude (Figs 10 and 11) [see also results on *Hemitragus jemlahicus* by Paré *et al.* (1996), disregarding one outlier population out of seven], which also corresponds to other observations on individual species referenced in Section 1. Finally, the finding of a high correlation between day length at conception in the wild and in captivity (Fig. 9) is strong evidence for a genetically fixed photosensitivity in ruminants that acts not only at the level of day-length changes (short-day or long-day breeders and refractoriness), but also at the level of absolute day length. To our knowledge, such strict dependence on absolute day length has not been demonstrated previously in ruminants, and is mostly considered a feature of arthropods and comparatively short-lived (and hence small) vertebrates (Bradshaw & Holzapfel, 2007). Experimental manipulation of reproductive activity in ruminants by artificial control of day length was usually not performed with the aim of detecting a specific absolute day length that triggers reproduction, but to detect patterns according to day-length change and refractoriness to long or short days (see Verme & Ozoga, 1987, for a typical example). Therefore, the result that reproductive activity is probably triggered by absolute day length in many seasonal wild ruminant species clearly warrants corroboration by experimental studies.

(*b*) *Resource availability*

There is overwhelming evidence that body condition (especially body fat stores), or in other words resource availability and the opportunity to accumulate fat reserves over a certain time period, will determine reproductive potential (Sadleir, 1969; Bronson, 1989). High resource availability and good body condition leads to earlier conceptions and births even in seasonally reproducing species (examples in Ogutu *et al.*, 2010; also see Section I). Our analysis of day length at the time of conception in free-ranging and captive populations (Fig. 9) yielded, as predicted, a numerically positive intercept, suggestive of slightly earlier conceptions in captivity - as would be expected because of the consistent provision with food. However, this effect was not significantly greater than zero, emphasizing that the influence of nutrition on seasonal breeders, though present in individual studies, is not strong enough to cause a systematic shift towards earlier conceptions and births in captivity. Again, more controlled experiments with defined day-length changes and defined levels of food provision would be required to accurately separate these effects.

When searching for triggers of reproductive seasonality, it is important to separate ultimate causes, such as favourable conditions at the time of parturition, from the proximate causes, which must be sought around the time of conception. Even though gestation period length can be adjusted to a certain degree according to actual climatic or resource conditions, the timing of conception—and hence, the timing of oestrus and rut—are the major proximate determinants of the timing of the birthing season (Ogutu *et al.*, 2010; Clements *et al.*, 2011). When investigating the effect of resource availability on birthing patterns, it is therefore important to consider these conditions at the time of conception—in ruminants, this means that the resource conditions of the previous season have to be linked to birthing patterns.

Several authors could demonstrate a correlation between rainfall, animal condition or other indicators of resource availability during the time of conception with the timing of either rutting events or birth patterns (Estes, 1976; Adams & Dale, 1998; Post, 2003; Moe *et al.*, 2007; Ryan, Knechtel & Getz, 2007; Ogutu *et al.*, 2010, 2011; Burthe *et al.*, 2011). Sometimes, confusion can occur as to whether authors refer to the birthing pattern coinciding with the rainfall pattern of the same year of the births, or of the preceding year. One consequence of resource-induced seasonality is that birth synchrony is higher after seasons with high rainfall, because a higher number of females will come into oestrus at the same time (Ogutu *et al.*, 2010). Another consequence is that reproductive seasonality may vary within a species, depending on the degree of resource seasonality different populations of that species are exposed to—either as compared between different free-ranging populations (Moe *et al.*, 2007) or as compared between free-ranging and captive populations (Pelt, 1967; Skinner *et al.*, 2002; Piening Schuler *et al.*, 2009; present study).

Periodic reproduction triggered by resources, and in particular rainfall events, is considered the least understood phenomenon in mammalian seasonality (Bronson, 2009). This may partly be due to the confusing finding that species differ in the timing of birthing periods in relation to the more or less regular rainfall events of the same season. By contrast, we suggest that the lack of a relevant pattern would probably disappear if one considered not the putative ultimate reason—births close to rainfall for maximum resource availability—but the probable proximate reason—conception at the time of optimal body condition, which should be close to the preceding season's rainfall, together with the gestation period of the species.

Several examples can be used to support this view. Hall-Martin, Skinner & Van Dyk (1975) found a conception peak in giraffe at the time of optimal nutritional status of females, whereas the resulting timing of birth did not provide newborns with optimal resources. Ryan *et al.* (2007) suggested that the comparatively long gestation period of African buffalo (*Syncerus caffer*) might be an adaptation to seasonality in the species' environment, leading, after an induction of oestrus by rainfall, to a birth of neonates close to the beginning of the next season's rainfall. On the one

hand, our own analysis suggests that the gestation period of African buffalo need not be considered peculiar due to the species low degree of reproductive seasonality; on the other hand, the authors themselves note that due to this long gestation period, African buffalo need to conceive very soon after parturition if they do not want to lose out on the next favourable resource cycle. Other species, in which oestrus, rut and conception are triggered by rainfall, might have shorter gestation periods (due to smaller body size), might give birth to their young somewhat earlier in relation to the next rainfall period, and might have more time between parturition and the time when the next conception needs to occur in order to make use of the next resource cycle. The fact that good body condition due to rainfall will trigger conception in many sympatric species at the same time will lead to a variation in birth peaks in relation to the following season's rainfall - because of the interspecific variation in gestation length. This could be a parsimonious explanation for the observation that sympatric cervid species in Nepal (Asher *et al.*, 1999) or sympatric ungulates in Southern Zimbabwe (Dasmann & Mossman, 1962) had very distinct birthing seasons (although their neonates should all thrive best at a similar time of year). It could also explain why smaller grazing species tended to give birth earlier (close to the peak protein concentration of young grasses) and larger species later (closer to the peak grass biomass) in the study of Sinclair *et al.* (2000*b*). These authors also wondered why oribi (*Ourebia ourebi*), although being a very small grazer, had a birth peak not around the peak of protein concentration in young grass (as the authors would expect based on their nutritional concept), but rather at the time of peak grass biomass, and speculated that this might be an adaptation to the necessity for hiding young in tall grasses. A more parsimonious explanation could be that conception might be triggered by young grass growth and that therefore the parturition peak occurs at the time of peak grass biomass - 210 days later (the oribi's gestation period; Jones *et al.*, 2009).

Recently, differences in the seasonal reproduction of sympatric Axis deer (*Axis axis*, seasonal birth peak) and gaur (*Bos gaurus*, no seasonal birth peak) in India have been explained as an adaptation to the higher nutritional requirements of the smaller species (Ahrestani *et al.*, 2011)—an ultimate reason. The proximate reason might simply be that the Axis deer have synchronized births triggered by monsoon rainfall; because of this species' shorter gestation period, enough time elapses after birth until the next period of high resources for the next conception, so that a seasonal pattern can emerge. The longer gestation periods of gaur are more likely to prevent conception at the time of high resources after a previous conception triggered by these events, which will by necessity lead to a more even spread of birth events across seasons. Reduced nutritional requirements of larger species, if existent, could act as a permissive factor that does not restrict conception to a certain time period (Ahrestani *et al.*, 2011); however, our finding that body mass did not significantly contribute to the relationship between seasonality and latitude, neither in the global analysis nor among African or non-African species (Table 4), does not suggest that permissive factors due to systematic changes in nutritional requirements with body mass are relevant for the evolution of reproductive seasonality.

Further insight into these phenomena could be generated if not only the length of the rainfall and vegetative periods, but also rutting and the body condition of the respective species over the course of these periods was monitored, to test whether species-specific adaptations in the timing of the onset of rut exist. Additionally, it would be interesting to compare various ruminant habitats with known rainfall and resource patterns, testing whether ruminant species composition in these habitats is determined by the relationship of gestation period (as mainly determined by body mass) to the lag periods between two periods of high resource availability. It could be hypothesized that species are favoured whose gestation period allows an optimal use of the respective periods of high resource availability without losing reproductive potential due to delays between parturition and the following conception (Kiltie, 1988).

Conceptually, one might argue that the resource-dependence of conception did not so much evolve as a response to a predictive trigger—in the sense that this year's rainfall might also indicate next year's rainfall -, but rather as a mechanism of reducing the energetic demands of reproduction during times of scarce resources. Note that the latter interpretation removes the element of prediction from resource-dependent reproduction, but shifts the focus to an 'emergency break' function that prevents parents from fatally depleting their own resources. Such a mechanism has been proposed previously by Owen-Smith (1988, p. 184) for white rhinoceros (*Ceratotherium simum*); he found evidence that high planes of nutrition were not so much stimulating reproduction, but that rather low planes of nutrition prevented it; similar findings on elephants are also provided by this author. Synchronised seasonality then simply ensues because after a period of scarcity, many adults will enter reproductive activity in the next season of high resource availability simultaneously. This view is also more compatible with current understanding of the hormonal modulation of reproduction by signals referring to body condition such as leptin (e.g. Zieba *et al.*, 2007).

(*c*) *Specific examples*

The peculiar case of the springbok (*Antidorcas marsupialis*), the only species that changed to a more seasonal birth pattern in captivity in this study, has already been noted by other authors for zoos in both hemispheres (Pelt, 1967; Skinner *et al.*, 2002). To date, a similar change of birth seasonality was only observed in domestic hoofstock from the tropics—i.e. Creole goats - which have a rather unseasonal reproductive pattern in the tropics, but demonstrate a marked seasonality when subjected to the large photoperiodic variation in the northern hemisphere (Chemineau *et al.*, 2004). Skinner *et al.* (1996) observed irregular rutting in springbok males but noted that the majority of ruts occurred closely to

the beginning of the long-day period after the southern-hemisphere winter solstice in June; by contrast, conception in our zoo population was concentrated during the short-day period of the northern-hemisphere year. Reasons for this discrepancy remain unclear, but could lie in the fact that the animals observed in the wild did not respond to photoperiodism but to resource cues. Later Skinner *et al.* (2001) observed spontaneous ovarian cycling in recently matured springbok ewes from November to June, i.e. in the short-day period of the southern hemisphere; the animals ceased cycling close to the summer solstice and started cycling again, after an interruption of about 4 months, during the following short-day period. These findings are easier to reconcile with the observations from captivity, and suggest that in the wild, there is a strong modulation of seasonal reproduction by resource availability, leading to variable conception dates. In captivity, because resources are continually provided, the photoperiodic signal is less modulated and hence seasonality more readily detected.

By contrast, the striking difference in seasonality between the free-ranging and the captive Nilgiri tahr (*Hemitragus hyloricus*) populations, with non-seasonal reproduction in captivity, do not support the hypothesis that reproduction is linked to photoperiod in this species. Rice (1988) suggested changes in photoperiod due to the monsoon (with short days due to clouded skies) as the proximate causes of seasonal reproduction in free-ranging Nilgiri tahr, but this should then also have an effect in temperate-zone zoos. In this species, reproduction is therefore probably only resource-constrained.

(6) Gestation length and reproductive seasonality

Several authors have noted the relevance of gestation period lengths for seasonal reproduction (Kiltie, 1988; Owen-Smith, 1988; Jabbour *et al.*, 1997). In particular, it has been suggested that smaller species might be forced to evolve particularly long gestation periods, in order to bridge the time between favourable rutting conditions and favourable birthing conditions (Jabbour *et al.*, 1997), and that large animals need to shorten their gestation period so that both parturition and the subsequent conception can both occur in the same (short) vegetation period; otherwise, they would lose one seasonal cycle for reproduction (Kiltie, 1988). The results of our study clearly support the latter concept, in that more seasonal ruminants have comparatively shorter gestation periods (Fig. 12). In contrast, there was no evidence for a systematic increase in gestation period with decreasing body mass in seasonal ruminants (i.e. the seasonality-body mass interaction was not significant when investigating the influence of both factors on gestation length).

It needs to be acknowledged that the concept of one assumed fixed gestation period length per species evidently does not reflect reality. The length of the gestation period can change, within a species, with parity (primiparous *versus* multiparous) and with the condition of the mother (and hence with variable environmental conditions), with the sex and the number of the offspring, and with conception date itself (reviewed in Clements *et al.*, 2011). While such fine-tuning of gestation periods does occur, it is nevertheless the timing of conception—and hence, the average gestation period of a species—that is the major determinant of the timing of the birthing season (Ogutu *et al.*, 2010; Clements *et al.*, 2011).

As seasonal environments have short periods of sufficient food supply, these time periods have to be used to full capacity by resident species. The mating season is often accompanied by a decreased food intake not only due to lack of time (Geist, 1974*a*; Lincoln & Short, 1980) but probably also as a side-effect of physiological processes associated with chemical cues of rut (Miquelle, 1990). It may be advantageous in seasonal environments to set this period to a time of the year when food supply is no longer at its optimum and body fat stores have accumulated maximally (Owen-Smith, 2002, pp. 156–158), so that no valuable opportunities for building up body reserves for the winter period are wasted. To achieve this goal, seasonal reproducing species of higher latitudes might shift conception and rut more to the end of the vegetative period, and hence closer to the next favourable period of parturition. It remains to be investigated whether differences between various taxonomic groups exist in the degree that gestation periods can be shortened. This characteristic may have made some ruminant groups particularly pre-adapted candidates for the occupation of seasonal habitats (in contrast to giraffids, camelids or perissodactyls) as suggested above.

On the other hand, a prolongation of gestation periods appears to be rare among ruminants. Increasing gestation length by the mechanism of delayed implantation—possibly a conserved characteristic in mammals (Ptak *et al.*, 2012) - has been documented in the roe deer (*Capreolus capreolus*) (Short & Hay, 1966). Note that the inclusion of this dramatic outlier affected the statistical results (Table 9). Delayed implantation was also suspected to occur in several other ruminant species such as the New World deer *Blastocerus* and *Hippocamelus* (not represented in this study) (Jabbour *et al.*, 1997), pudu (*Pudu puda*) (Bubenik *et al.*, 2000), and in the Père David's deer (*Elaphurus davidianus*) (Brinklow & Loudon, 1993). Our findings reinforce such suspicions insofar as both the pudu and the Père David's deer are among the more seasonal species that have, for their body size, comparatively long gestation periods; the same is true for the pronghorn antelope (*Antilocapra americana*) (Fig. 12A). In the pronghorn, foetal growth might be delayed as compared to other ungulates (fig. 1 in Robbins & Robbins, 1979), and yet unconfirmed reports of an increasing gestation period with latitude (Buechner, 1950) are also compatible with delayed embryonic development. Future studies might detect retarded embryonic growth, or delayed implantation, in these species.

V. CONCLUSIONS

(1) We expressed the degree of birth seasonality of species as a continuous variable: the time period in which a certain percentage of all offspring are born.

(2) Latitude of geographical origin of species' was found to be the only significant factor influencing the degree of birth

seasonality, i.e. the birth seasons become shorter (animal species become more seasonal) with increasing latitude of geographical origin.

(3) As only about 11% of the tested species distinctively changed their birth seasonality pattern in captivity when compared to wild populations, the birth season length in zoos can be seen as a good predictor for birth season length in the wild for temperate species.

(4) It is well recognized that the evolved adaptation of using specific photoperiodic cues for the timing of reproductive activity in temperate species can lead to problems under current global warming scenarios. In generally warmer conditions, plants will tend to emerge earlier, while reproduction cued to photosignals stays inert and thus becomes out of synch with the beginning of forage availability, with potentially deleterious effects (Post & Forchhammer, 2008; Post *et al.*, 2008; Bronson, 2009). Changes in breeding phenology, linked to variation in resource availability due to warmer climate, have been documented in both seasonal and aseasonal breeders (Burthe *et al.*, 2011; Moyes *et al.*, 2011). The degree to which ruminants will be affected by the mismatch between photoperiod and resource availability will depend on the speed at which adjustments of the photoperiodic responses can evolve—or to which degree less-seasonal species can replace more-seasonal species in their respective ecosystems.

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VIII. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Appendix S1. Birth seasonality and biological characteristics of 110 ruminant species.

Appendix S2. Mating season of wild populations.

Appendix S3. Phylogenetic tree used for the phylogenetic generalized least-squares method (PGLS).

Appendix S4. References for Appendices S1–S3.

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Appendix S1. Birth seasonality and biological characteristics of 110 ruminant species.

	Biological characteristics							Seasonality of reproduction						
										Birth windows				
	Body mass (kg)[a]	Sexual size dimorphism[ah]	%grass	Mating type[ah]	Mother-young relationship[ar]	Gestation length (d)[a]	Mid latitude[a]	Seasonality free ranging	Seasonality captivity	BPB50	BPB50 Julian start day	BPB80	BPB80 Julian start day	*N*
Tragulus javanicus	1.9	0.89[an]	0[d; e]	1[ai]	2	159	-7.4 [au]	5[au]	5	180	345	285	125	565
Tragulus napu	5.3	0.98[an]	0[f; e]	1[ai]	2	154	4.2	5[av]	5	175	65	285	45	399
*Antilocapra americana**	45[b]	1.19	15[d; g]	3	2	248	37.2	1[aw; ax]	1	25	150	45	140	1208
Giraffa camelopardalis	965	1.57	0[d; h]	2	2[as]	455	-4.6	4[ay; az]	4	155	120	275	365	3301
Okapia johnstoni	230	0.94[fq]	0[d]	2[ai]	2	443	-1.6	5[ba]	4	150	150	255	140	428
Moschus moschiferus	13	1.09	4[i]	1	2	176	53.4	1[bb]	1	20	155	50	145	164
*Alces alces**	462	1.27	2[d; g]	2	1	235	58.5 [fa]	2 (1)[bc; bd]	1	20	130	40	125	652
*Capreolus capreolus**	22[b]	1.08	9[d; g]	3	2	298	51.3	2[be]	1	25	140	40	125	457
Hydropotes inermis	13	1.14	50[d; j]	1	2	175	28.9	2 (1)[bf]	1	20	145	35	135	767
*Rangifer tarandus**	113[b]	1.45	36[d; g]	3	1[at]	222	64.6	1[bg; bh]	1	25	120	50	115	3527
*Odocoileus hemionus**	85	1.36	11[d; g]	2	2	203	41.8	1[bi; bj]	1	20	155	45	145	544
*Odocoileus virginianus**	76	1.66	9[d; g]	2	2	201	21.9	2 (1)[bk]	1	20	150	55	140	2378
Mazama americana	21	1.00	1[d]	2	2	225	-9.9	4[bl]	5	175	170	280	210	230
Pudu puda	9.5	1.00[an]	3[k]	1[j]	2	210	-43.7	2[bm]	2	40	120	105	110	715
Ozotoceros bezoarticus	35	1.14[an]	75[l]	2	2	220	-21.9	4 (3, 2)[bn]	3	75	55	160	20	99
Axis axis	70	1.78	70[d; g]	2	2	227	17.3	5 (4, 2)[bo; bp]	4	145	355	265	315	5284
Axis porcinus	37	1.34	73[m]	2	2	220	20.6	2[bq; bp]	4	135	65	270	45	903

*Cervus elaphus**	241	1.33	47[d; g]	3	2	236	46.4	2 (1)[br; bs; bb]	1	30	150	75	130	4950
*Cervus nippon**	53	1.32	50[d; g]	3	2	224	34.0	2[bt; bu]	2	55	145	140	80	3755
Cervus albirostris	161	1.63[j]	98[n]	3[c]	2	263	33.7	2[bb]	2	40	160	80	150	221
Elaphurus davidianus	166	1.35	75[d; j]	3	2	286	34.5[fb]	1[bv]	1	25	100	55	90	2045
Cervus eldii	95	1.57	65[d]	3[ai]	2	240	18.9	2[bw]	2	45	270	95	255	1130
Cervus duvaucelii	169	1.63[an]	75[o]	3[ai]	2	245	25.8	2[bx]	2	65	140	110	125	1537
Cervus alfredi	46	1.32[c]	50[c]	3[c]	2	243	10.5	2 (1)[by]	4	130	250	245	165	160
Cervus unicolor	176	1.32	28[m, p]	3	2	246	12.0	2[bp]	4	105	280	230	205	560
Cervus timorensis	66	1.38	75[c]	3	2	250	-7.4	3[bz]	3	65	255	225	155	195
*Dama dama**	55[b]	1.43	46[d; g]	3	2	230	48.3	2 (1)[ca; cb]	1	20	160	45	155	4459
*Dama mesopotamica**	74	1.43[c]	46[c]	3[c]	2	225[fc]	33.6[fm]	2[cc]	2	35	125	70	120	241
Muntiacus muntjak	18	1.13[an]	10[d]	1	2	210	11.8	5[bp]	5	170	140	280	275	368
Muntiacus reevesi	14	0.80	10[f; g]	1[ai]	2	214	27.2	4[cd]	4	135	115	265	95	3294
Elaphodus cephalophus	23	1.25[fv]	10[q]	1[ai]	2	181	27.9	2[ce]	3	90	105	205	95	203
Cephalophus dorsalis	20	0.96[ak]	0[r]	1[ak]	2	238	1.1	5 (4)[ak; cg]	5	150	105	275	105	174
Cephalophus silvicultor	62	0.73[fs]	1[s, r]	1[al]	2	234	-1.9	5 (4)[al]	5	125	290	255	290	214
Cephalophus maxwellii	8.4	0.94[ak]	1[r]	1[ak]	2	205	9.1	4[ch]	5	145	365	270	240	257
Cephalophus monticola	4.9	0.87[an]	0[r]	1[l]	2	205	-12.5	5 (4)[ak; cg]	5	155	100	265	75	316
Bos frontalis	800[b]	1.49	66[t]	2	1	274	15.4	4[ad; cj; ck]	4	145	110	265	70	908
Bos javanicus	667[b]	1.67[fs]	80[d]	2[ai]	1	297	8.2	2[cl]	4	145	40	250	350	885
*Bos grunniens**	500	2.11[fw]	86[n]	2[ai]	1	274	34.3	2[cm]	3	85	115	160	90	1818
*Bison bison**	625	1.65	84[d; g]	2	1[as]	283	44.3	2[cn]	2	45	115	115	105	4474
*Bison bonasus**	676	1.70[fs]	68[d; g]	2[ai]	1	266	51.1[fn]	2[co]	2	70	130	150	120	1694
Bubalus bubalis	930	1.50[ft]	80[u]	2[ai]	1	320	21.0	2[cp]	4	110	185	235	100	549
Bubalus depressicornis	257	1.08[ft]	4[v]	2[c]	1	296	-1.3	5[cq]	5	155	190	270	70	277
Syncerus caffer	593	1.30	90[d; g]	2	1	337	-8.8	4 (3, 2)[cr; bh]	5	175	185	290	185	937
Boselaphus tragocamelus	182	1.44	29[v; d; h]	3	2	248	22.4	2[ad]	3	105	195	240	90	2971
Tetracerus quadricornis	19[b]	1.06[fs]	9[v]	1[ai]	1	207	22.3	4[cs]	5	100	340	220	350	175
Taurotragus derbianus	646	1.55[an]	5[r]	2[c]	2	275[fd]	8.8	3[ct]	3	85	180	170	130	164
Taurotragus oryx	563	1.47	10[fj; fk; fl]	2	2	271	-10.1	4[cu; cr]	4	115	55	235	5	3546
Tragelaphus strepsiceros	206	1.51	5[d; g]	2	2	271[fr]	-7.0	4 (3, 2)[cv; cw]	3	70	195	175	180	2510
Tragelaphus imberbis	94	1.14	10[d; h]	2	2	222	3.9	5[cx]	4	140	255	270	255	826
Tragelaphus eurycerus	271	1.25	20[w]	2	2[as]	285	2.1	5[cy]	4	140	5	250	340	1595
Tragelaphus spekii	76	1.89	67.5[d]	2	2	241	-3.3	5[ay]	4	160	365	275	320	3165
Tragelaphus scriptus	43	1.58	10[u]	2	2	183	-9.4	5[cz; ay]	5	165	5	270	10	187

Tragelaphus angasii	88	1.83[an]	20[d]	2	2	220	-22.0	5 (4)[da; db]	5	170	15	275	295	2057
Kobus ellipsiprymnus	202	1.33	80[d; h]	3	2	270	-6.5	4[cr; bh]	4	150	145	275	20	2841
Kobus leche	89	1.31	95[r]	3	2	230	-14.2	4 (2)[dc; db; ay]	4	150	95	270	10	2139
Kobus megaceros	86	1.41[ft]	95[r]	3[ai]	2	237[fe]	8.0	2[dd]	4	135	295	235	275	1527
Kobus kob	80	1.47	95[d]	3	2	255	6.2	5[de; df]	5	170	95	280	45	450
Redunca fulvorufula	30[b]	1.03	99[d; h]	2	2	223	-12.3	5 (4)[dg; cw]	4	90	165	205	100	220
Aepyceros melampus	53	1.33	60[d; g]	3	2	197	-12.9	4[dh; da; di; cr]	3	55	135	190	120	2648
Antidorcas marsupialis	34	1.21	30[d]	3	2	170	-20.7	4[dj]	2	85	110	235	95	1856
Antilope cervicapra	38[b]	1.09[an]	61[v; d; g]	3[ai]	2	167	18.8	2[dk]	4	145	45	265	65	7042
Gazella dorcas	16	1.31[ci]	25[r]	3[ai]	2[at]	172	23.6	2[dl; dm]	4	160	40	275	45	815
Gazella spekei	20[b]	1.28[fs]	50[r]	3[ai]	2	179	6.5		4	145	95	270	80	309
Gazella arabica	24	1.31[c]	50[c]	3[ai]	2	170[c]	13.7		4	135	125	245	120	406
Gazella subgutturosa	27	1.18[cf]	50[f]	3[ai]	2	160	32.1	2 (1)[dn]	1	25	120	75	90	1807
Gazella cuvieri	20[c]	1.44[ft]	50[c]	3[c]	2	170[ff]	30.4		4	105	45	230	15	529
Gazella leptoceros	24[b]	1.30[ft]	50[r]	3[ai]	2	167	24.8		3	50	75	200	65	1127
Gazella thomsonii	23	1.20	86[w; h]	3	2	166	1.9	4[bh]	3	115	100	250	90	1960
Nanger dama	73[b]	1.33[fs]	48[r]	3[ai]	2	195	20.2	4 (3, 2, 1)[do]	4	130	170	250	70	2747
Nanger soemmerringii	42	1.35[fs]	50[r]	3[c]	2	193	9.8		3	95	190	220	115	265
Nanger granti	56	1.45	50[d; g]	3	2	191	0.3	5 (3)[bh; dp; cx]	4	125	140	250	140	1031
Litocranius walleri	39	1.45	0[d; h]	3	2	204	3.0	5[dq]	5	150	145	265	125	552
*Saiga tatarica**	38[b]	1.39	26[y]	3	2	148	46.5	1[dr]	1	15	130	30	120	414
Madoqua guentheri	4.6	0.82[am]	5[u]	1[am]	2	175	4.3	4 (2)[am; dp]	4	170	205	260	95	266
Madoqua kirkii	4.9[b]	0.93	17[r]	1	2[as]	171	-6.6	4 (2)[ds; dp]	4	165	285	255	255	652
Neotragus moschatus	5.6	0.93[an]	0[d]	1[an]	2	180	-13.3	4[dp]	5	170	45	275	305	292
Oreotragus oreotragus	14	1.00	5[u]	1	2	214	-7.8	4[dp]	4	150	180	270	120	212
Addax nasomaculatus	96	1.50[aj]	80[r]	3[ai]	2	263	20.5	(4)[dt; du]	4	135	360	245	340	3080
Oryx gazelle	195[b]	1.10	82[d; h]	3	2	274	-8.3	4[cz]	4	155	35	265	360	2748
Oryx leucoryx	76	1.06[an]	75[r]	3[ai]	2	240	20.6[fo]	4[dv]	4	130	20	240	330	1340
Oryx dammah	200	1.10[fs]	75[r]	3[ai]	2[as]	248	16.2	(4)[dw]	4	125	85	240	365	3957
Hippotragus niger	236	1.08	93[d]	3	2	273	-13.6	2[dx; ay; dy]	4	155	105	270	25	2555
Hippotragus equinus	264	1.02	85[r]	3	2	278	-4.6	5 (4)[dy; ay]	4	155	50	270	340	1031
Alcelaphus buselaphus	161	1.07	97[d; h]	3	2	243	5.8	4[cr; bh]	3	90	105	195	95	365
Damaliscus lunatus	78	1.18	99.3[u]	3	1	238	-16.5	2[dz; bh]	3	65	115	165	100	166
*Damaliscus pygargus**	85[b]	1.11[an]	100[d]	3[ai]	1	241	-29.5	2[ea; eb; ec]	3	65	130	155	120	1593
Connochaetes taurinus	199	1.35	90[d; g]	3[ai]	1[at]	251	-15.6	1 (2)[ed; cr; ay]	2	50	155	125	130	1652

*Connochaetes gnou**	157	1.29[an]	81[r]	3[ai]	1	257	-28.8	1[ee]	2	50	165	110	120	471
*Budorcas taxicolor**	295	1.18[ao]	30[c]	3[ao]	1	236	30.2	2[ef; bb]	2	60	35	135	15	271
*Ovis orientalis musimon**	50[c]	1.51[fu]	69[u]	2	1	153[fg]	41.2[fp]	1[eg; eh]	2	45	75	90	55	3351
Ovis orientalis gmelini	50[b]	1.59[fu]	69[d]	2	1	158[fh]	36.1[fp]	1[ei]	1	15	130	30	125	769
*Ovis orientalis vignei**	52	1.54[fu]	70[u]	2	1	165	34.2[fp]	1[ej]	1	20	105	40	100	748
*Ovis canadensis**	75	1.43	67[g]	2	1	177	40.5	1[ek]	1	25	125	55	105	1239
*Ovis dalli**	70	1.57	56[w; g]	2	1	172	60.6	1[el; em]	1	30	125	85	95	1161
*Capra aegagrus**	47	1.70	28[u]	2	1	156	33.6	2[en]	3	45	100	150	55	1499
*Capra ibex**	72[b]	2.11[an]	60[w; g]	2[ai]	1[at]	168	45.8	1[eo]	1	20	140	45	125	1517
*Capra sibirica**	130	2.04[x]	50[z]	2[ai]	1	175	43.5	1[ep; eq]	1	20	135	45	125	986
*Capra caucasica**	58	1.57[ft]	80[aa]	2[ai]	1	155	42.3	2[er]	1	20	135	40	125	858
*Capra cylindricornis**	58	1.66[an]	47.5[ab]	2[ab]	1	155	42.1[es]	2[es]	1	20	145	40	135	246
Capra nubiana	48	2.36[fu]	60[c]	2[ai]	1	150	23.5	2 (1)[et]	1	30	85	55	75	1095
Capra falconeri	54	2.27[an]	60[c]	2[ai]	1	168	33.9	2 (1)[eu]	1	20	140	40	130	2458
Hemitragus hylocrius	74	2.00[fs]	64[ac]	2[ai]	1	186	10.0	2[ev]	5	150	135	260	50	178
Hemitragus jemlahicus	68	2.03	75[d; ad]	2	1[at]	196	30.1	2[bb]	2	30	150	55	140	1436
Pseudois nayaur	52	1.35	68[ae]	2	1	160	34.4	1[ae]	1	30	165	60	150	259
Ammotragus lervia	94	1.46	42[af]	2	1	156	24.8	1 (2)[ew]	2	55	70	145	30	4804
Rupicapra rupicapra	33	1.21	74[d; g]	3[ai]	1	178	43.5	1[ex; ey]	1	25	130	55	110	449
*Oreamnos americanus**	72	1.39	61[g]	2	1	181	54.1	1[ez]	1	15	145	35	135	714
Naemorhedus caudatus	27	1.11[an]	50[c]	2[c]	1	180[fi]	42.0	2[bb]	2	45	135	90	125	264
Capricornis crispus	43	1.00	3.1[ag]	2[ap]	1	213	36.8	2[ap]	2	30	125	90	125	97
*Ovibos moschatus**	313	1.47	62[g]	3[aq]	1	256	71.7	2[aq]	2	30	135	70	125	637

References (see online Appendix S4):

[a] Jones *et al*. (2009); [b] Ernest (2003); [c] estimated from close relative as sufficient data were not available; [d] Hofmann *et al*. (2008); [e] Nordin (1978); [f] Clauss *et al.* (2008); [g] Van Wieren (1996); [h] Owen-Smith (1997); [i] Green (1987); [j] Geist (1998); [k] Eldridge *et al.* (1987); [l] Jackson & Giulietti (1988); [m] Dinerstein (1982); [n] Harris & Miller (1995); [o] Wegge, Shrestha & Moe (2006); [p] Padmalal, Takatsuki & Jayasekara (2003); [q] Sheng & Lu (1982); [r] Gagnon & Chew (2000); [s] Gautier-Hion, Emmons & Dubost (1980); [t] Chetri (2006); [u] Clauss *et al.* (2010); [v] Pujaningsih [et al.] (2009); [w] Solanki & Naik (1998); [x] Fedosenko & Blank (2001); [y] Bannikov *et al.* (1967); [z] estimated from Fedosenko & Blank (2005); [aa] Weinberg (2004); [ab] Weinberg (2008); [ac] Sumithran (1997); [ad] Schaller (1967); [ae] Wang & Hoffmann (1987), [af] Ogren (1962); [ag] Ochiai (1999); [ah] Weckerly (1998); [ai] Grzimek (1979/1980); [aj] Krausman & Casey (2007); [ak] Wilson (2005); [al] Lumpkin & Kranz (1984); [am] Kingswood & Kumamoto (1996); [an] Loison *et al.* (1999); [ao] Neas & Hoffmann (1987); [ap] Jass & Mead (2004); [aq] Lent (1988); [ar] Stoner, Caro & Graham (2003); [as] Ralls, Kranz & Lundrigan (1986); [at] Ralls, Lundrigan & Kranz (1987); [au] Duckworth *et al.* (2008); [av] Lutz (2001); [aw] Kitchen (1974); [ax] Buechner (1950); [ay] Ansell (1960); [az] Fairall (1968); [ba] Bodmer & Rabb (1992); [bb] Unknown Author (2005); [bc] Haagenrud & Markgren (1974); [bd] Stringham (1974); [be] Linnell & Andersen (1998); [bf] Kirkwood (2007); [bg] Lent (1966);

[bh] Sinclair, Mduma & Arcese (2000); [bi] Jordan (1976); [bj] Anderson & Olof (1984); [bk] Illige (1951); [bl] Gardner (1971); [bm] Pollard (1999); [bn] Ungerfeld *et al.* (2008); [bo] Loudon (1988); [bp] Mishra & Wemmer (1987); [bq] Dhungel & O'Gara (1991); [br] Guinness, Clutton-Brock & Albon (1978); [bs] Clutton-Brock, Guinness & Albon (1983); [bt] Evtushevsky (1974); [bu] Maruyama *et al.* (1975); [bv] Wemmer *et al.* (1989); [bw] Worrel (2004); [bx] Ferraino & Yahnke (2007); [by] Key (2003); [bz] Reyes (2002); [ca] Chapman & Chapman (1975); [cb] Sterba & Klusak (1984); [cc] Perelberg *et al.* (2003); [cd] Pei *et al.* (1995); [ce] Lundrigan & Oas (2003); [cf] Kingswood & Blank (1996); [cg] Kranz & Lumpkin (1982); [ch] Aeschlimann (1963); [ci] Tom-Tov (1995); [cj] Vairavel (1998); [ck] National Research Council (1983); [cl] Choquent (1993); [cm] Zi (2003); [cn] Rutberg (1984); [co] Balčiauskas (1999); [cp] Singh, Singh & Bains (1985); [cq] Miller (2002); [cr] Spinage (1973); [cs] Leslie & Sharma (2009); [ct] Altan (2000); [cu] Pappas (2002); [cv] Simpson (1968); [cw] Kingdon (1982); [cx] Leuthold & Leuthold (1975); [cy] Turkalo & Turkalo (1999); [cz] Skinner, Moss & Skinner (2002); [da] Anderson (1979); [db] Leuthold (1977); [dc] Sayer & Lavieren (1975); [dd] Corrie & Yahnke (2004); [de] Modha & Eltringham (1976); [df] Leuthold (1967); [dg] Irby (1979); [dh] Murray (1982); [di] Moe, Rutina & Du Toit (2007); [dj] Skinner *et al.* (1996); [dk] Prakash (1960); [dl] Mendelssohn & Yom-Tov (1987); [dm] Yom-Tov, Mendelssohn & Groves (1995); [dn] Kingswood & Blank (1996); [do] Cano & Cano (2007); [dp] Spinage (1986); [dq] Penfold (2005); [dr] Sokolov (1974); [ds] Kingswood & Kumamoto (1997); [dt] Manski (1991); [du] Asa (1996); [dv] Vié (1996); [dw] Morrow (1999); [dx] Sekulic (1978); [dy] Wilson & Hirst (1977); [dz] Child, Robbel & Hepburn (1972); [ea] Du Plessis (1972); [eb] David (1973); [ec] David (1975); [ed] Estes (1976); [ee] Richter (1971); [ef] Wang *et al.* (2005); [eg] Langbein, Streich & Scheibe (1998); [eh] Langbein (1998); [ei] Valdez, Cardenas & Sanchez (1991); [ej] Awan & Festa-Bianchet (2006); [ek] Shackleton (1985); [el] Bowyer & Leslie (1992); [em] Bunnell (1980); [en] Edge (1990); [eo] Stüwe & Grodinsky (1987); [ep] Dmitriev (1938); [eq] Roberts (1977); [er] Adler & Bar-Oz (2009); [es] Weinberg (2002); [et] Habibi (1997); [eu] Coblentz (1980); [ev] Rice (1988); [ew] Gray & Simpson (1980); [ex] Hardenberg (2000); [ey] Boschi (2003); [ez] Rideout & Hoffmann (1975); [fa] Henttonen *et al.* (2008); [fb] Zhigang & Harris (2008); [fc] Cavendish (2001); [fd] Angwafo (2006); [fe] Falchetti & Mostacci (1993); [ff] Furley (1986); [fg] Reavill (2000); [fh] Flores-Foxworth *et al.* (1995); [fi] Mead (1989); [fj] Codron *et al.* (2007); [fk] Watson & Owen-Smith (2002); [fl] Sponheimer *et al.* (2003); [fm] Rabiei (2010); [fn] Olech (2008); [fo] IUCN SSC Antelope Specialist Group (2008); [fp] Valdez (2008); [fq] ISIS data were used; [fr] Dittrich (1972); [fs] Bro-Jørgensen (2008); [ft] Bro-Jørgensen (2007); [fu] Polák & Frynta (2009); [fv] Carranza (1996); [fw] Leslie & Schaller (2009).

Body mass: median of the mean male and female body mass; sexual size dimorphism: ratio between body mass of males and females; % grass: percentage of grass in the natural diet of a species; Mating type: 1 = monogamous, 2 = males follow more than one female but no harem or territory is defended, 3 = harem or territory is defended; Mother-young relationship: 1 = follower, 2 = hider; Mid latitude: centre of the latitude range that a species inhabits; Seasonality of reproduction (categories for free ranging and captive) from 1: highly seasonal to 5: aseasonal species (for details see text and Fig. 2; note that for comparisons between free-ranging and captive populations, the reported category not in parentheses was used, which were considered most typical for the species; categories in parentheses represent other patterns described for the species in the literature); BPB: birth peak breadth, measure of the degree of reproductive seasonality as number of days (measured as consecutive 5-day blocks) which included the required percentage of birth (50% or 80%); Julian start day: first Julian day (of the year) of the respective BPB; *N*: number of observed birth events in the captive population.For species that are marked with an asterix (*) data on the exact start of mating season and the latitude of origin of at least one free-ranging population were available (Appendix S2). These data were used for further analyses.

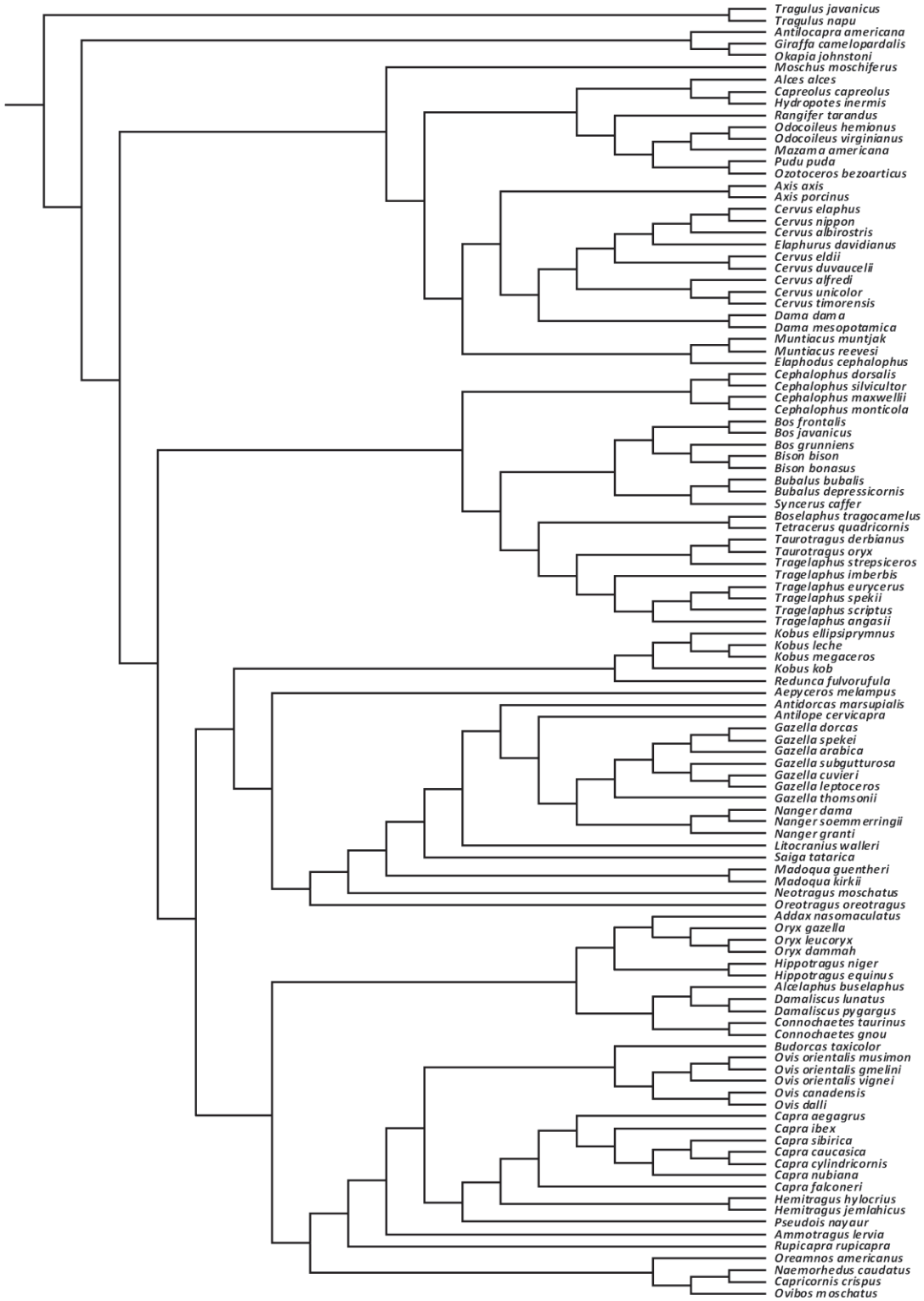
Appendix S2. Mating season of wild populations

Start of mating seasons for populations of seasonal ruminants for which the exact start date of the mating season (sometimes calculated as first observed birth event minus the average gestation length) *and* the exact mid latitude of the origin of the population were available.

Species	Start of mating season (Julian day)	Latitude of origin	Reference
Antilocapra americana	267	40.1	Fairbanks (1993)
Alces alces	267	63.8	Bowyer, Van Ballenberghe & Kie (1998)
Capreolus capreolus	289	63.7	Linnell & Andersen (1998)
Rangifer tarandus	269	62.2	Reimers, Klein & Sørumgård (1983)
Odocoileus hemionus	329	32.9	Bowyer (1991)
Odocoileus virginianus	300	47.1	Carstensen Powell & DelGiudice, 2005)
Cervus elaphus	256	57	Guinness *et al.* (1978)
Cervus nippon	252	35	Asada & Ochiai (1996)
Dama dama	280	37	Braza, San Jose & Blom (1988)
Dama mesopotamica	225	33	Perelberg *et al.* (2003)
Bos grunniens	183	32.5	Zi (2003)
Bison bison	193	47.3	Rutberg (1984)
*Bison bonasus**	282	56.1	Balčiauskas (1999)
Saiga tatarica	339	48	Bekenov, Grachev & Milner-Gulland (1998)
Damaliscus pygargus	260[a]	-25.9	Du Plessis (1972)
Connochaetes gnou	246[a]	-30.5	Vrahimis & Kok (1994)
Budorcas taxicolor	160	33.7	Wang *et al.* (2005)
Ovis orientalis musimon	277	40.4	Santiago-Moreno *et al.* (2001)
*Ovis orientalis vignei**	231	25	Awan & Festa-Bianchet (2006)
*Ovis canadensis**	332	58.8	Bunnell (1982)
*Ovis dalli**	323	64	Rachlow & Bowyer (1991)
Capra aegagrus	224	25.6	Edge (1990)
Capra ibex	336	46.5	Giocometti & Ratti (1994)
Capra sibirica	305	45	Fedosenko & Blank (2001)
Capra caucasica	363	43.4	Dinnik (1887)
Capra cylindricornis	369	42.8	Weinberg (2002)
Oreamnos americanus	324	54	Côté & Festa-Bianchet (2001)
*Ovibos moschatus**	205	60.1	Lent (1988)

Species marked with an asterix (*) are outliers. Statistical analyses were performed with and without these species.
[a]corrected for transformation to the northern hemisphere.
See Appendix S4 for references.

Appendix S3. Phylogenetic tree used for the phylogenetic generalized least-squares method (PGLS).



Appendix S4. References for Appendices S1-S3.

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Curriculum vitae

Name	Philipp Zerbe
Geburtsdatum	07.05.1985
Geburtsort	Offenbach am Main
Nationalität	Deutsch

1992-1996	Grundschule (Kolpingschule, Aschaffenburg,Deutschland)
1996-2002	Friedrich-Dessauer-Gymnasium (Aschaffenburg, Deutschland)
2002-2004	Kantonsschule Reussbühl (Kanton Luzern, Schweiz)
17.06.2004	Matura, Kantonsschule Reussbühl (Kanton Luzern, Schweiz) Schwerpunkt: Mathematik-Physik
2004-2010	Studium Veterinärmedizin, Vetsuisse-Fakultät Zürich, Schweiz
14.10.2010	Diplom Veterinärmedizin, Vetsuisse-Fakultät Zürich, Schweiz
2010-2012	Anfertigung der Dissertation unter Leitung von PD Dr. med. vet. Marcus Clauss am Departement für Kleintiere, Klinik für Zoo-, Heim- und Wildtiere Vetsuisse-Fakultät Universität Zürich Direktor: Prof. Dr. med. vet. Jean-Michel Hatt
2011-2012	Internship/Assistenz Abteilung für Kleintierfortpflanzung Klinik für Fortpflanzungsmedizin, Universität Zürich, Schweiz
2012-	Veterinary Research Fellowship, Preclinical Service Focus Area Surgery, AO Research Institute Davos, Schweiz

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